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Journal of the Fisheries Research Board of Canada

Announcement

The December issue of previous volumes of this Journal contained a subject–author index and list of all publications issued during a given calendar year.

The index for 1972 publications is being incorporated into an amalgamated index covering the years 1965 to 1972. This amalgamation will be published as a number in the FRB Bulletin series in early 1973, and distributed free to all Journal recipients, including subscribers. Additional copies will be available through the Office of the Editor.

The contents for this volume appears at the back of this issue for library binding purposes.

J. C. Stevenson
Editor and Director
of Scientific Information

Eggs and Larvae of Northern Sand Lance (*Ammodytes dubius*) from the Scotian Shelf

J. S. Scott

Fisheries Research Board of Canada
Biological Station, St. Andrews, N.B.

Scott, J. S. 1972. Eggs and larvae of northern sand lance (*Ammodytes dubius*) from the Scotian Shelf. J. Fish. Res. Bd. Canada 29: 1667–1671.

Eggs from stomachs of yellowtail flounder (*Limanda ferruginea*) from Emerald Bank, south of Nova Scotia, were identified as those of northern sand lance, *Ammodytes dubius*. They were larger than those of other *Ammodytes* species, with a mean diameter of 1.05 mm. Ovarian eggs from ripe *A. dubius* were smaller (mean diameter 0.7 mm) with a unimodal distribution of egg diameters, indicating a single spawning each season.

Larvae were widespread and abundant on the Scotian Shelf from February to April. They hatched at about 4-mm length and grew to about 25-mm length between February and May on Emerald Bank. Growth rates decreased to the north. Numbers and distribution of melanophores changed with larval length, but showed no differences in number at given length between geographical areas. Change in numbers of anal, caudal, and dorsal fin rays followed a pattern similar to that of corresponding melanophores.

Scott, J. S. 1972. Eggs and larvae of northern sand lance (*Ammodytes dubius*) from the Scotian Shelf. J. Fish. Res. Bd. Canada 29: 1667–1671.

L'auteur identifie comme étant ceux du lançon du nord (*Ammodytes dubius*) les oeufs trouvés dans l'estomac de la limande à queue jaune (*Limanda ferruginea*) provenant du banc Emeraude, au sud de la Nouvelle-Ecosse. D'un diamètre moyen de 1.05 mm, ils sont plus gros que ceux de toute autre espèce d'*Ammodytes*. Les oeufs prélevés à même l'ovaire mûr d'*A. dubius* sont plus petits (diamètre moyen 0.7 mm), et leurs diamètres ont une distribution unimodale, ce qui indique une seule fraie par saison.

Les larves sont dispersées en grand nombre sur le plateau néo-écossais à partir de février jusqu'en avril. Elles mesurent environ 4 mm à l'éclosion et atteignent une longueur d'environ 25 mm entre février et mai sur le banc Emeraude. Le rythme de croissance ralentit vers le nord. Le nombre et la répartition des mélanophores varient avec la longueur des larves, mais ne révèlent aucune différence numérique, pour une longueur donnée, entre les régions. Le nombre de rayons des nageoires anale, caudale et dorsale varie de la même façon que les mélanophores correspondants.

Received June 26, 1972

In January 1967 and February 1968 large numbers of fish eggs were found in stomachs of yellowtail flounder (*Limanda ferruginea*) caught on Emerald and Western banks on the Scotian Shelf, where good sand lance catches were frequently made. Occurrence of the eggs in yellowtail indicated they were demersal and this, together with time and area of occurrence, suggested they might be eggs of winter spawning sand lance, *Ammodytes dubius* (Scott 1968).

Ammodytes dubius eggs have not been described previously but identification was made possible by the excellent condition of the eggs from yellowtail stomachs and the late-stage embryonic larvae contained in them.

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Very brief descriptions of *A. dubius* larvae have been given (Einarsson 1951). They are indistinguishable from those of *A. marinus*, a Greenland and European lance (Macer 1967). More detailed description is now possible from study of the eggs and of larvae taken in plankton hauls. The latter were examined mainly to check for differences which might indicate separate sand lance populations on the Scotian Shelf, but they also provided new data on larval growth and development, particularly pigmentation, which has been used to distinguish larvae of various *Ammodytes* species (Corbin and Vati 1949). Richards (1965) described *Ammodytes* larvae from various parts of the northwest Atlantic and found the same basic characteristics from all areas. Her data included only 11 specimens from

Nova Scotia (collected in 1885) and none from the Gulf of St. Lawrence.

Materials and Methods

Fertilized eggs were separated from stomach contents of yellowtail flounder immediately after capture. Ovarian eggs were dissected from ripe sand lance that had been frozen immediately after capture and thawed in the laboratory. Larvae were captured with 6-ft Isaacs–Kidd midwater trawls and Neuston nets on research cruises through 1967–70. Fertilized eggs and larvae were preserved in 8% formalin. Maximum and minimum egg diameters were measured with a stereomicroscope with screw micrometer eyepiece. Larvae, often sinuously curved, were measured by tracing their longitudinal axes with the aid of a camera lucida, then measuring the trace with a map-measurer. On conversion, this gave actual length to within 1 mm. Numbers of melanophores in different pigmentation areas of larvae were recorded. Totals of 100 ovarian eggs and 107 eggs from yellowtail stomachs were measured and lengths and melanophore counts recorded from 615 larvae.

Results and Discussion

Eggs

Eggs from yellowtail stomachs were in late stages of development, with well-formed larvae. Embryos resembled closely those of *Ammodytes* which were abundant in near-surface waters over much of the Scotian Shelf. Identification of *A. dubius* was confirmed from descriptions of sand lance larvae by Einarsson (1951), Richards (1965), and Macer (1967).

Occurrence of eggs with adherent sand grains in yellowtail stomachs indicated that they were demersal and adhesive, as those of other Ammodytidae, thus not usually available to plankton nets. They were similar to those of North Sea *A. tobianus* (Furnestin 1939) and North American *A. hexapterus* (= *A. americanus*) (Williams et al. 1964): demersal, adhesive, and subspherical, usually with a single oil globule. However, they differed from eggs of other *Ammodytes* in size, mean diameters ranging 0.87–1.23 mm, as compared with 0.7–0.8 mm for *A. tobianus* (Furnestin 1939) and 0.67–0.91 for *A. hexapterus* (Williams et al. 1964). Mean maximum and minimum diameters of *A. dubius* eggs were 1.02 and 0.97 mm, respectively (N = 107). Greater egg size may reflect greater size of *A. dubius* (Scott 1968) compared with closely related, possibly conspecific *A. hexapterus* (Richards 1965).

Frequency distribution of diameters of larvaceous eggs was compared with that of eggs from ripe female *A. dubius* caught in October 1968 (Fig. 1). Maximum diameters of ovarian eggs, after freezing and subsequent thawing, ranged 0.63–0.82 mm with a mean at 0.70 (N = 100), considerably smaller than the fertilized eggs. Both frequency distributions were unimodal. The unimodal distribution for ovarian eggs confirms that *A. dubius* spawns once each spawning season, as does its European counterpart *A. marinus* (Macer 1966) and, probably, other sand lance species (Reay 1970).

Largest excised larvae from eggs were about 4 mm in length, similar to that of *A. hexapterus* at hatching. Larval morphology, and numbers and distribution of melanophores in the embryo, made identification to genus relatively easy.

Larvae

Larvae were abundant and widely distributed in surface and near-surface plankton over the banks in 1967–70 (Fig. 2), particularly in February and

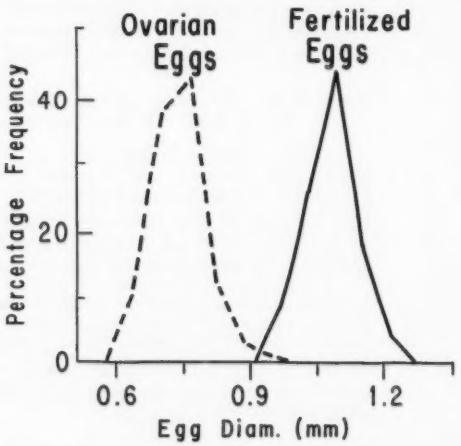

FIG. 1. Frequency distributions of maximum diameters of ovarian and fertilized eggs of *Ammodytes dubius*.

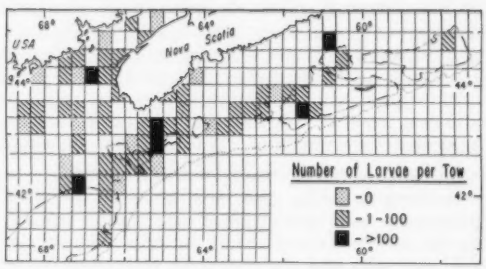

FIG. 2. Numbers of *Ammodytes dubius* larvae caught per 15-min plankton tow with Isaacs-Kidd midwater trawl on Scotian Shelf and vicinity in 1967–70.

TABLE 1. Means and standard deviations of lengths of *Ammodytes* larvae from different Banks on the Scotian Shelf, in February 1969 and May 1968 (number examined in brackets).

Area	Mean lengths (*mm*)	
	Feb. 1969	May 1968
Emerald	6.7±1.9(130)	24.7±9.8(31)
Western	6.8±1.2(110)	16.9±5.8(44)
Sable Island		12.5±7.4(6)
Middle	6.2±1.4(596)	12.9±5.3(55)
Banquereau		6.1±1.6(82)

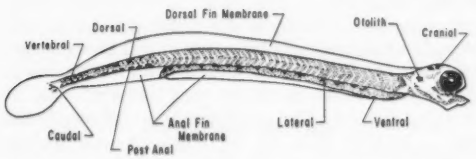

FIG. 3. *Ammodytes dubius* larva (semi-diagrammatic) showing pigmentation areas.

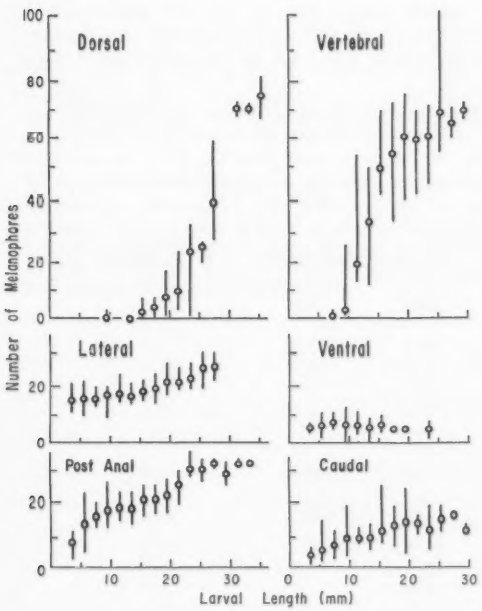

FIG. 4. *Ammodytes dubius*. Ranges and mean numbers of melanophores per 2-mm larval length group from Emerald Bank.

March. Sameoto (MS 1971) recorded abundant and widespread occurrence of *Ammodytes* larvae on the Scotian Shelf during larval herring surveys in the spring of 1969. They were present until July, but not later.

Length-frequency distributions of larvae collected at different times and from various areas of the Scotian Shelf through 1967–70 were insufficient for comparison of growth rates in different areas, but sequences in May 1968 and February 1969 (Table 1) indicate a trend of decreasing mean lengths from Emerald Bank to Banquereau. This indicates different hatching times or decreasing growth rates to the northeast and little mixing of larvae between

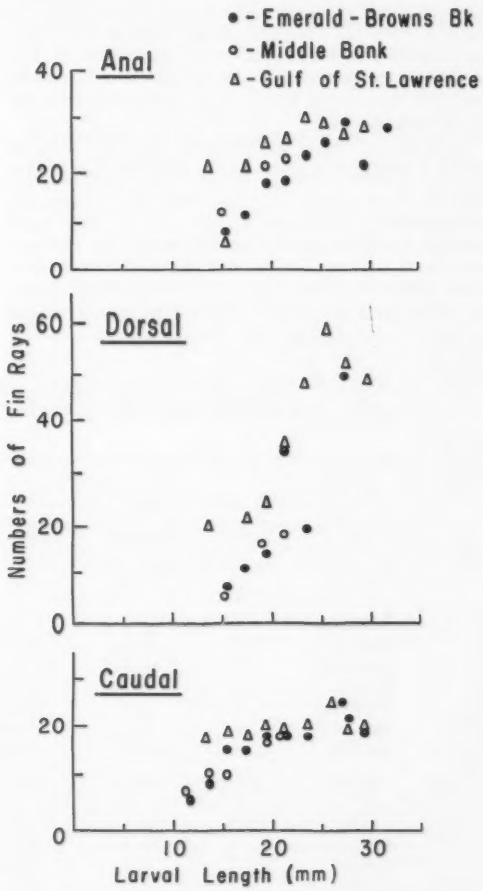

FIG. 5. *Ammodytes dubius*. Mean numbers of fin rays per 2-mm larval length group from samples from different areas of Scotian Shelf and Gulf of St. Lawrence

the areas sampled. Differences in adult fish size (Scott 1972) support different growth rates.

There were insufficient data for preparation of larval growth curves but monthly mean lengths of all samples from Emerald Bank indicate the rate of growth (mm): February, 6.9 ± 1.9 (180); March, 14.4 ± 3.6 (100); April, 20.1 ± 4.5 (118); and May, 22.9 ± 7.2 (80). Mean larval length increased from 7.1 to 24.7 mm on Emerald Bank during February to May 1968, an average monthly rate of about 5.9 mm — about half that of *A. hexapterus* from Chesapeake Bay (Norcross et al. 1961).

Larvae of different lengths were characterized by differences in numbers and distribution of melanophores. Nomenclature used to describe pigmentation is shown in Fig. 3. It differs slightly from that of Corbin and Vati (1949) and Macer (1967). The first of these spots appear before hatching and their numbers increase in a distinctive pattern throughout larval development.

Changes in mean numbers of melanophores in various pigmentation areas during larval growth are shown in Fig. 4. Ventral, postanal, and caudal melanophores appeared in the embryo and were present in all larvae. Ventral fin membrane pigment was never present. Dorsal and cranial melanophores were observed as early as the 5–6-mm length group in a few specimens, but were not generally present in fish of less than 10 mm.

Ventral melanophores were almost constant in number during larval growth, mean counts ranging between 5.0 and 7.3 in larvae up to 24 mm, after which they could not be distinguished. Lateral melanophores showed a steady increase in number from a mean of 15.4 in larvae in the 3–4-mm length group to 26.0 in the 27–28-mm length group. Dorsal and vertebral melanophores increased rapidly in number with larval length and became too numerous to count after about 30 mm. Caudal and cranial melanophores increased slowly in number up to about 30 mm.

The number of postanal melanophores increased with fish length up to about 30 mm and levelled off when about equal to the definitive anal fin ray number, although the latter was not reached until a later stage in growth (Fig. 5).

Increase in numbers of anal, dorsal, and caudal fin rays followed a similar pattern to those of postanal, dorsal, and caudal melanophores, respectively, although anal and caudal fin rays appeared later in development than the corresponding melanophores (Fig. 4 and 5). Patterns for Emerald and Middle banks were similar but the Gulf of St. Lawrence sample was rather distinct, with higher numbers at lesser lengths. This was possibly due to the small sample size (21 specimens).

Larvae longer than 8 mm had prominent and characteristic melanophores that did not increase in number with larval length. These included a single,

TABLE 2. Mean number of melanophores in 9–10 and 15–16 mm length groups of *Ammodytes dubius* larvae on Nova Scotian Banks and Gulf of St. Lawrence (number of larvae examined in brackets).

Larval length (*mm*)	Browns	Emerald	Western	Middle	Banquereau	Gulf of St. Lawrence
9–10		(28)	(8)	(40)	(5)	(1)
Lateral	–	17.1	17.0	16.1	15.5	–
Post-anal	–	18.0	19.1	16.6	18.6	15.0
Ventral	–	6.6	5.6	5.8	–	0.0
Dorsal	–	0.07	0.4	0.2	1.5	0.0
Vertebral	–	2.7	10.0	0.0	–	–
Caudal	–	9.2	9.6	6.8	–	7.0
Cranial	–	0.9	0.8	3.4	0.8	1.0
15–16	(7)	(11)	(14)	(3)	(1)	(14)
Lateral	16.5	18.3	16.8	16.3	–	17.8
Post-anal	17.1	20.9	18.8	18.0	15.0	19.8
Ventral	2.7	6.2	3.0	5.0	–	5.5
Dorsal	0.0	2.1	3.1	1.0	–	0.3
Vertebral	41.5	49.4	46.3	28.0	–	32.4
Caudal	9.0	12.0	8.6	10.3	–	10.0
Cranial	1.7	2.9	2.3	2.0	–	1.9

large dorsal spot immediately posterior to the head, one to four spots on each operculum, and a single large spot on each developing otolith cavity that appears to be the precursor of the dense aggregation of melanophores on the otolith sac in adult fish.

Melanophore numbers and larval length for samples from various areas were closely related (Table 2). On the basis of melanophore numbers in relation to larval length, there is no evidence for existence of distinct groups of larvae in different areas.

Fecundity of *A. dubius* was not estimated but, by analogy with other *Ammodytes* species, it is assumed to be high. In the early months of the year, *Ammodytes* is the predominant larval fish in the plankton on the Scotian Shelf, Newfoundland (Serebryakov 1965; Sameoto MS 1971), and west Greenland Banks (Smidt 1971). Even allowing for high mortalities, this abundance (Serebryakov 1965) suggests that parent stocks are among the larger components of the fish biomass of the northwest Atlantic.

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Morphological and Meristic Variation in Northwest Atlantic Sand Lances (*Ammodytes*)

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Scott, J. S. 1972. Morphological and meristic variation in northwest Atlantic sand lances (*Ammodytes*). J. Fish. Res. Bd. Canada 29: 1673–1678.

Morphological characteristics of *Ammodytes* species from Greenland to New England showed little variation from area to area, except for mean and maximum lengths which increased offshore from north to south and from inshore to offshore. Meristic numbers (dorsal and anal fin rays, vertebrae) were fairly uniform for offshore stocks, but reduced values in Gulf of St. Lawrence and off Cape Cod bridged the gap between offshore (*A. dubius*) and inshore (*A. hexapterus*) values which had previously been used to differentiate the species.

Weight–length relations conformed to the standard weight–length equation and were similar over the Nova Scotia and Newfoundland grand banks. There was a considerable difference between prespawning and postspawning fish, indicating a 30% loss in weight during spawning.

There appeared to be a close relation between morphological and meristic variation, and environment. Changes in fish size and meristic numbers corresponded to changes in water temperature, but observed ranges in meristic numbers were much greater than experimentally induced changes in other species, and genetic variation between stocks is difficult to discount.

Scott, J. S. 1972. Morphological and meristic variation in northwest Atlantic sand lances (*Ammodytes*). J. Fish. Res. Bd. Canada 29: 1673–1678.

Les caractères morphologiques des diverses espèces d'*Ammodytes* exhibent très peu de variations régionales depuis le Groenland jusqu'à la Nouvelle-Angleterre, à l'exception des longueurs moyennes et maximales qui, au large, augmentent du nord au sud, et du littoral vers la pleine mer. Les caractères méristiques (rayons de la dorsale et de l'anale, vertèbres) sont relativement constants chez les stocks hauturiers, mais les valeurs inférieures observées dans le golfe Saint-Laurent et au large du cap Cod chevauchent sur celles des lançons du large (*A. dubius*) et celles des lançons du littoral (*A. hexapterus*), valeurs jadis utilisées pour distinguer les espèces.

Les relations poids–longueur concordent avec l'équation poids–longueur normale et sont identiques pour les bancs de la Nouvelle-Ecosse et les bancs de Terre-Neuve. Il y a une grande différence entre les poissons capturés avant et après la fraie, signe d'une perte de poids de 30% pendant la fraie.

Il semble y avoir une corrélation étroite entre les variations des caractères morphologiques et méristiques et l'environnement. Les variations de la taille du poisson et des comptages méristiques correspondent aux variations de température. Toutefois, les intervalles observés dans les comptages méristiques sont beaucoup plus grands que ceux provoqués expérimentalement chez d'autres espèces, et il est difficile de ne pas tenir compte de la possibilité de variations génétiques entre les stocks.

Received June 26, 1972

The taxonomic characteristics of northwest Atlantic Ammodytidae have received considerable attention, particularly from Richards et al. (1963), Scott (1968), and Winters (1970). These studies revealed differences, particularly in anal and dorsal fin ray and vertebral numbers, between inshore stocks found in coastal waters, bays and estuaries, and northern stocks found on offshore banks. These groups were originally given specific status, *Ammodytes hexapterus* for the inshore (southern) group and *A. dubius* for the offshore (northern) group (Richards et al. 1963). Overlap of ranges of meristic numbers and correlation of these numbers with environmental conditions have raised doubts about the validity of the two species and point towards existence of a single species, possibly also conspecific with *A. marinus*, the major Greenland and European lance.

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As well as meristic differences between groups of lance from major regions (New England coast, Scotian Shelf, west Greenland, Newfoundland coast, and Grand Banks), there were differences in size and growth rate between samples of *Ammodytes* from these regions, and between individual banks on the Scotian Shelf (J. S. Scott in preparation). Differences appeared to be related to environment, probably temperature, and indicated isolation of local groups of sand lance. This isolation might induce local variation in meristic and morphological characteristics other than growth, which would be useful in population identification.

To determine the extent of such local variation, certain characteristics of samples of *Ammodytes* from different areas of the northwest Atlantic were examined, including weight–length relations, which have not been reported previously for northwest Atlantic lances. The results of the investigation complement previous work and indicate factors influencing the occurrence of sand lance and its availability in fishing operations.

Materials and Methods

All material from the Nova Scotia banks was obtained during Fisheries Research Board of Canada groundfish research cruises through 1967–70, using #36 or #41 Yankee otter trawls with ¼-inch mesh codend liners. For comparison with other regions, samples of *A. dubius* were obtained from the Newfoundland Banks, Gulf of St. Lawrence, west Greenland, Georges Bank, and off the New England coast, using a variety of fishing gears.

Thirty-six samples of adult sand lance, comprising 2739 specimens, were examined. They were frozen immediately after capture and examined after thawing in the laboratory. Total length to the nearest millimeter, sex, maturity (Scott 1968), and date and position of capture were recorded and otoliths were preserved in glycerin. Vertebral counts (by dissection or from X-ray photographs), dorsal and anal fin ray numbers, standard and fork lengths, body depth, head length, and snout length were recorded for whole samples as required or for representative subsamples when sample size was inconveniently large. Weights of individual fish were recorded in the latter part of the program. Details of otolith measurement and preparation of growth curves are given elsewhere (J. S. Scott in preparation).

Results

Morphology

A variety of morphological characteristics was used for comparison of samples from different areas, including fish length and ratios of fish length to body depth, head length and otolith length, head to snout length, and otolith width to otolith length.

Total length was used in all comparisons of fish length with other measurements. Conversion of total length to standard or fork length was simple, if required, as they were directly proportional and their relation varied very little between samples from different areas. Ranges from all samples, as percentages of total length, were: fork length: 96.5–98.0, standard length: 92.6–93.7.

Representative lengths of fish from each area are shown in Table 1 as mean lengths of whole sample and as mean length of fish in the top 5-cm length-group of each sample (maximum length). The general trend on the offshore banks is an increase in size from north to south, except for anomalies in the Newfoundland Grand Banks and Banquereau–Middle bank areas. Mean lengths show an increase to Georges Bank then a sharp decrease to Cape Cod, which is comparable to Middle Bank, and then to the exceptionally small fish from inshore on the New England coast at Newburyport. Maximum lengths showed a similar pattern except that highest values were in the Sable Island–Emerald Bank area in the central part of the Nova Scotia banks, and there was a slight decrease to Browns Bank and Georges Bank to the south. The small sample from the Gulf of St. Lawrence had values similar to Newfoundland samples.

Differences in representative lengths of fish between areas correspond to differences in growth rates (J. S. Scott in preparation). However, mean and maximum lengths of samples from a given area may vary greatly depending on gear used and whether or not there is size segregation in the species sampled. There is evidence of the latter in Newfoundland material, in which three samples had mean lengths of 16.05, 18.85, and 24.49 cm, respectively, with the length ranges of both low and high samples falling within the length range of the middle sample. However, this was exceptional, and on the Nova Scotia banks ranges, means, and maximum sizes were surprisingly consistent as exemplified by samples from Emerald Bank that had mean lengths of 26.23, 25.03, 24.76, 25.03, 24.17, 25.51, and 25.09 cm with an exceptional low of 20.57 cm in a sample with a very large size range (13–32 cm) and an exceptional number of small fish. Respective maximum lengths were 29.21, 29.40, 30.25, 27.68, 31.00, 27.00, 27.93, and 29.77 cm.

Nova Scotia banks samples fell into two distinct groups, one of fish with mean lengths 18.34–18.77 cm from the Banquereau–Middle bank area, and the other, with mean lengths 23.99–26.93 cm, from the Sable Island–Emerald–Browns banks area. The differences were persistent and not due to mesh selection, as they were found in samples taken by the same vessel using the same gear in different areas.

TABLE 1. Mean and maximum lengths of *Ammodytes* from different areas of northwest Atlantic.

	No.	Mean length (*cm*)	SD	Maximum length[a] (*cm*)
Greenland	56	17.87	3.11	22.50
Newfoundland (S.E. Grand Banks)	268	19.97	3.71	24.90
Gulf of St. Lawrence	12	20.31	3.25	24.50
Banquereau	141	18.63	2.80	21.21
Middle Bank	127	18.29	2.44	22.25
Sable Island Bank	397	23.38	3.00	30.75
Emerald Bank	622	24.46	3.55	29.15
Browns Bank	248	26.78	1.71	27.52
Georges Bank	19	27.00	1.05	27.00
Cape Cod	50	18.20	2.54	23.68
Newburyport	100	12.70	3.08	14.66

[a]Mean of top 5-cm length-group.

Fish length/depth ratios ranged from 11.91–16.1, the lower figure being for southern inshore samples, in accordance with Richards et al. (1963), who found that southern lances are deeper-bodied than northern. However, the ratio for samples from Emerald Bank ranged from 15.9 for prespawners to 11.9 for spent fish, indicating a very considerable increase in depth at given length during maturation.

Mean head length/snout length ratios fell in a narrow range, 2.8–3.2, and showed no trend or difference between areas, except for a Gulf of St. Lawrence value of 4.0 for the small sample examined (12).

The fish length/head length ratio increased slightly from Banquereau (5.5) to Browns (5.9) and was slightly lower than in the coastal lances sampled (5.3–5.5).

The fish length/otolith length ratio remained about the same from Greenland to Georges Bank (100–111) but was lower in the southern inshore lances (83–91). In general, the northern otoliths were wider than the southern, width/length ratios decreasing from 0.52 in Greenland to 0.47 in Massachusetts. There was a slight difference between the Banquereau (0.51) and Browns–Sable Island banks (0.49) groups.

MERISTICS

Meristic characters of northwest Atlantic sand lances were examined in detail by Richards et al. (1963), and Scott (1968) described material from southern Nova Scotia banks. Samples from the northern Nova Scotia banks, Gulf of St. Lawrence, and Georges Bank have not been described previously. They are included in Fig. 1, giving ranges and means of dorsal and anal fin rays, and vertebral numbers for areas covered in the present study.

There was surprising consistency in mean counts for samples from Georges Bank to Greenland (*A. dubius*), except for the Gulf of St. Lawrence which was slightly lower on all counts. Values for lance taken offshore from Cape Cod lay between those for Georges Bank (*A. dubius*) and inshore Newburyport (*A. hexapterus*). These findings are in keeping with the general trend of increasing meristic counts from south to north and inshore to offshore (Richards et al. 1963; Winters 1970). Inshore lance have been observed on the Nova Scotia coast but only one specimen has been obtained. This was similar to the Cape Cod material: length, 17.7 cm; dorsal fin rays, 57; anal fin rays, 30; and vertebrae, 68.

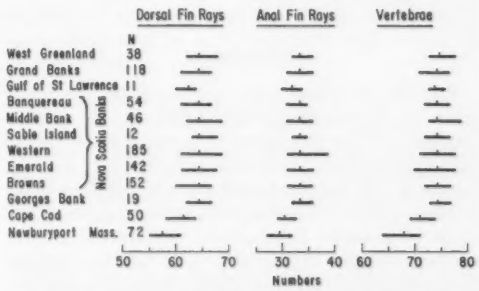

FIG. 1. Ranges and means of dorsal and anal fin ray and vertebral numbers of *Ammodytes* from different areas of northwest Atlantic.

Weight–length Relation

The weight–length data for *A. dubius* were assumed to conform to the general relationship $W = AL^B$ (W = fish weight in grams; L = fish length in cm). This was confirmed by plotting mean weight against fish length, giving a characteristic weight–length curve (Fig. 2A). Values of coefficient A and B, for all samples combined (N = 925) from Emerald Bank, were A = 0.002, B = 2.994. Macer (1966) obtained A = 0.0025, B = 3.068 for *A. marinus* from the North Sea. A sample from Newfoundland Grand Banks (N = 219) gave A = 0.003, B = 2.943, so there does not appear to be any notable difference in length–weight relation of *A. dubius* between areas. There was no obvious difference between male and female fish.

On inspection, ripening fish were obviously deeper- and wider-bodied than postspawners and were expected to be heavier at a given length. This was confirmed by length–weight data (Fig. 2B) showing the relevant curves for Emerald Bank fish at selected maturity stages. The curve for postspawners reflects their lower weight–length ratio.

Further emphasis on the effect of maturation is given by comparison of mean weights of 24.5–25.4-cm length-group fish from Western–Emerald–Browns area for months on each side of the spawning period in 1969:

Month	No.	Mean weight (*g*)
July	51	40.7
September	22	46.3
November	7	43.1
December }	main spawning period	
January }		
February	26	29.5
March	43	29.4

There was a 30% loss in weight during spawning in the length-group selected.

Discussion

Samples of *Ammodytes* examined in this study were more remarkable for uniformity of characteristics than for differences that might be attributed to different species. Only two characteristics, meristic numbers and length, varied enough between areas to suggest that different species, or even populations, might be involved. Relation of body depth to length, which was noted by Richards et al. (1963) to be the most significant difference between inshore and offshore lances, was shown to vary so much with maturity that perhaps it cannot be considered a reliable criterion of taxonomic status.

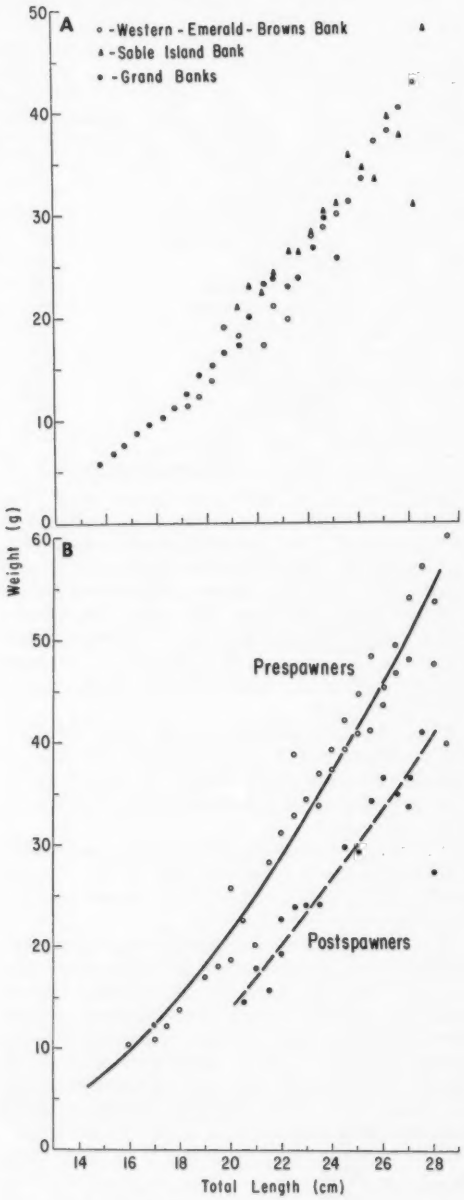

FIG. 2. Plots of mean weights against length for *Ammodytes dubius* from (*A*) all samples combined from Nova Scotia Banks and Newfoundland Grand Banks, and (B) prespawners and postspawners from Emerald Bank.

The wide range of meristic numbers from New England to Greenland is noteworthy. Without intermediate values found in Cape Cod and Gulf of St. Lawrence material, there was a distinct separation into inshore and offshore groups as noted by Richards et al. (1963) and Winters (1970). The intermediate values eliminate the distinction but do not help in indicating the factor or factors that determine the meristic numbers in different areas.

A similar situation exists regarding maximum fish length, although this appears to be more sensitive to its determinant(s) than meristics, to judge from the variation found in the limited area of the Scotian Shelf. The relations between meristics and size in different areas are so similar that they suggest that the same factor or factors are responsible for both.

The northward decrease in size noted in offshore lance is expected in relation to lower water temperature and slower growth in higher latitudes. The difference in mean and maximum sizes between the northwest part of the Nova Scotia banks (Banquereau–Middle banks) and the southwest (Western–Emerald–Browns banks) corresponds to differences in mean annual bottom temperatures (J. S. Scott in preparation).

Richards (1965) suggests temperature and salinity as the determinant factors for meristic differences and Winters (1970) suggests higher spawning temperatures on Newfoundland Grand Banks as a possible explanation for anomalous values for vertebral counts in Newfoundland material. Higher temperatures may also explain the high values for mean and maximum fish lengths in Newfoundland material compared to more southerly Banquereau samples.

A difficulty in explaining differences in meristic numbers between fish from different areas on the basis of temperature alone arises from the fact that there is no information on the stage of development at which the numbers are determined. Experimental results indicate that determination takes place before hatching in sea trout (Tåning 1952) and herring (Hempel and Blaxter 1961).

Meristic numbers of inshore and offshore lances differ by values much in excess of those induced in the experiments with sea trout and herring, in a temperature range of about 3–14 C. The evidence strongly suggests that some factor or factors other than temperature are involved in determining meristic numbers. Indeed, the range of meristic counts in northwest Atlantic *Ammodytes* is so much greater than experimental changes of environment have induced in other fishes that genetic determination of meristic characters is likely.

Weight–length relations were unremarkable and samples from different areas could not be distinguished on this basis. The relatively low ratio of weight to length reflected the elongated body form of the species. Data were not recorded for inshore lance from New England but their length to depth ratio (11.9) is so close to Nova Scotia banks values (12.2–16.1) that they are thought to conform to the general situation. Comparison of prespawning and postspawning samples (Fig. 2B) emphasized the considerable effect of maturation on weight. The 30% difference between prespawners and postspawners indicated exceptionally large gonad development and, considering the moderately sized egg, high fecundity.

Persistent differences in morphology and meristics between groups of *Ammodytes* indicate that the groups are restricted in movement both between inshore and offshore areas and along the coast or offshore banks. Data above indicate separate stocks on the New England coast, banks off Cape Cod, Nova Scotia coast, Nova Scotia banks (and Georges Bank?), Gulf of St. Lawrence, Newfoundland Grand Banks, and Greenland. Within some of these divisions there are local subdivisions indicated by differences in growth rates, such as on the various banks of the Scotian Shelf. A similar situation was noted in the North Sea by Macer (1966).

Isolation of groups with different meristic characters is complete, at least from the time that characters are determined, otherwise differences would disappear. As the characters are determined very early in life, certainly before the larvae leave the plankton, isolation must be effective even when the larvae are subject to dispersion by tidal and oceanic currents. Such a situation may give rise in time to genetically distinct populations and eventually to separate subspecies or species.

Although morphometrics and meristics have provided an indication of taxonomic status of different *Ammodytes* groups, these criteria are not sufficient in themselves. Genetic (electrophoretic) and cultural (interbreeding, larval rearing) techniques might be more rewarding in a fish showing such variability of characters.

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Evidence for Expatriate Populations of the Lanternfish *Myctophum punctatum* in the Northwest Atlantic[1]

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ZURBRIGG, R. E., AND W. B. SCOTT. 1972. Evidence for expatriate populations of the lanternfish *Myctophum punctatum* in the northwest Atlantic. J. Fish. Res. Bd. Canada 29: 1679–1683.

Myctophum punctatum populations in the Northwest Atlantic are probably expatriate, being composed almost exclusively of very large individuals and lacking postlarvae. Females do not possess maturing or gravid ovaries. The apparent physiological stress on these fish is reflected by irregular and sometimes regressive growth evidenced in their scales, otoliths, and subopercles.

ZURBRIGG, R. E., AND W. B. SCOTT. 1972. Evidence for expatriate populations of the lanternfish *Myctophum punctatum* in the northwest Atlantic. J. Fish. Res. Bd. Canada 29: 1679–1683.

Les populations de *Myctophum punctatum* de l'Atlantique Nord-Ouest sont probablement des expatriées, constituées qu'elles sont presque entièrement de très grands individus, et dépourvues d'un stade postlarvaire. Les femelles ne possèdent pas d'ovaires en voie de maturation ou gravides. Le stress physiologique que ces poissons semblent subir se réflète dans une croissance irrégulière et parfois même régressive, tel que démontré par les écailles, les otolithes et les sous-opercules.

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THE mesopelagic fishes of the Myctophidae, including *Myctophum punctatum*, form an important link in food chains (e.g. as prey for cod, pollock, and swordfish (Popova 1962; Rojo 1967; Scott and Tibbo 1968)); hence, knowledge of their biology is pertinent. *Myctophum punctatum* is commonly caught off the Canadian east coast, yet its ecology remains essentially unknown. This study provides evidence that the species does not reproduce in this region, despite the abundance of large adults. Thus, the total species distribution is relevant and described below.

Myctophum punctatum occurs over deep water near the edge of the continental shelf from Greenland and Labrador to Cape Hatteras on the western side of the Atlantic, being limited seaward by the Gulf Stream. It is also known from off Iceland, the Shetlands, Norway, and Denmark, and is extremely common in the Bay of Biscay region, around the Straits of Gibraltar, and in the Mediterranean. *Myctophum punctatum* is resident around the Azores and strays south along the African Coast to Cape Blanc and the Canaries.

Materials and Methods

The origins of the specimens used for this work are diverse.

One hundred collections (1154 specimens) were taken, principally by the *A. T. Cameron*, between July 1946 and November 1964. The gear used were otter trawls in the course of fishery resource investigations in the late spring, summer, and autumn.

Some 381 specimens from Fisheries Research Board vessels were captured off Georges Bank, along the continental slope of Nova Scotia, in the Gulf of St. Lawrence, and east of the Grand Banks with a variety of nets; including neuston nets, 6- and 10-ft Isaacs–Kidd Midwater Trawls, and commercial nets. Although these collections include some samples from February through June, the bulk of the material was gathered in the summer and early autumn from 1966 to 1969.

[1]Based on a thesis submitted in partial fulfillment of the requirements for the degree of Master of Science at the Department of Zoology, University of Toronto.

Printed in Canada (J2190)

In July of 1968, 773 specimens were taken by the M/V *Brandal* north, east, and south of the Grand Banks and Flemish Cap using a large Engel trawl (vertical opening = 10 m).

These collection localities are plotted in Fig. 1.

Two hundred and fifty-five specimens were taken in slope water from Georges Bank northward in Woods Hole cruises; 573 specimens from the Azores, Gibraltar, and the Mediterranean during *Atlantis II* cruise 49 in May–June 1969; and 35 specimens from the northeast Atlantic during R/V *Chain* cruise 82 in May 1969.

Other miscellaneous material examined included 3 specimens each from south of Iceland (December 21, 1963) and west of the British Isles (January 25, 1964), stored in the Amsterdam Museum; 11 specimens from the Bay of Biscay captured in 1961, loaned from the National Museum of Canada; and 1 specimen from the Laurentian Channel captured in November 1960, also from the National Museum of Canada.

To be certain that the species under study was that described as *M. punctatum*, measurements and counts were made on a sample of 100 specimens from Canada's continental slope and 20 from Gibraltar, in accordance with Hubbs and Lagler (1958), gill raker counts excepted. All rudimentary gill rakers were counted, and the raker straddling the upper and lower limbs was counted separately. The morphometrics of the northwest Atlantic specimens are similar to published values, but a few counts give slightly different values than those in the literature (Jordan and Evermann 1896–1900; Taning 1918; Fowler 1936; Bolin 1959). Thus, pectoral fin rays are 13–15 (vs 13–14), upper gill rakers 6–8 (vs 6–7), anal rays not less than 20 (vs 19), and dorsal rays commonly 14, rarely 13 (vs 12–13). Branchiostegal rays number 8–10 and may be asymmetrical (not quoted in the literature). The AOp photophores are commonly 3 and 4 (vs 4, rarely 3, Fraser-Brunner 1949).

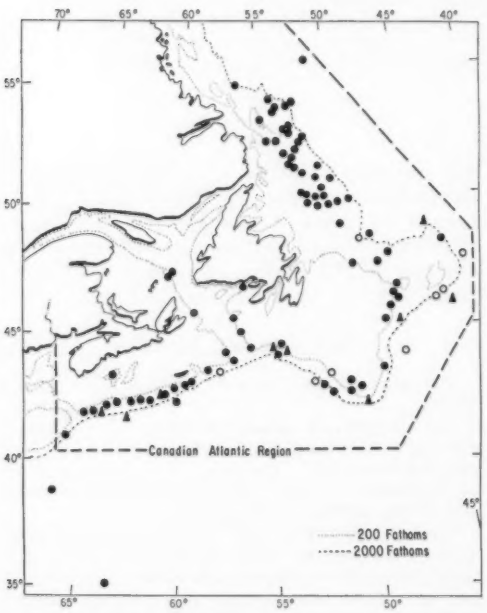

FIG. 1. Collection localities of *M. punctatum* in Canadian Atlantic waters. (Adults only, black circles; juveniles only, open circles; adults and juveniles together, triangles).

Females in all collections were examined to determine the condition of the eggs and ovaries. Some ovaries were used for sectioning and staining with haematoxylin and eosin (Fig. 2).

Otoliths were removed from the right side of the crania, subsequently cleaned, and placed into a solution of 50% glycerine, 40% water, and 10% ethanol. Otoliths were viewed by transmitted light with a binocular microscope and hyaline rings were counted (Fig. 3, 4, and 5). Frequently the first hyaline ring was obscure. Therefore, the ring counts all start with the second hyaline ring (i.e. the first recognizable hyaline ring in all otoliths) to achieve standardization of counts.

Results

Sexual Dimorphism

Northwest Atlantic *M. punctatum* develop sexual luminous plates on the caudal peduncle at 45–50-mm SL, the male having 1–4 (mean 1.3) dorsal plates and the female 2–5 (mean 2.9) ventral ones. Males average smaller than females (Fig. 3). The sexual plate distinction is often used in the literature for sexual determination but is seldom based, as in this study, on dissection. Specimens from an actively reproducing population near Gibraltar initiate development of the caudal plates at only 35-mm SL and have ranges of 2–4 (mean 2.8) in males, and 3–5 (mean 3.7) in females.

Individuals from the northwest Atlantic over 50-mm SL without plates, or with both a dorsal and ventral plate, are rare and number less than 10 in over 2500 specimens examined. These fish have the gonads reduced to minute threads of tissue.

Reproduction

The ovaries of *M. punctatum* caught off Canada's east coast are small and finely granular with only small oocytes, 0.05–0.10 mm in diameter. In histological appearance, the oocytes have either undergone little vitellogenesis or have degenerated (Fig. 2 a, b, c). Large, egg-filled ovaries with oocytes 0.20–0.25 mm in diameter are possessed by females captured in slope water east off the United States (Fig. 2 d).

Ripe ovaries, with eggs as large (0.40–0.43-mm diameter) as those described by Taning (1918), have not been found in any *M. punctatum* from the northwest Atlantic.

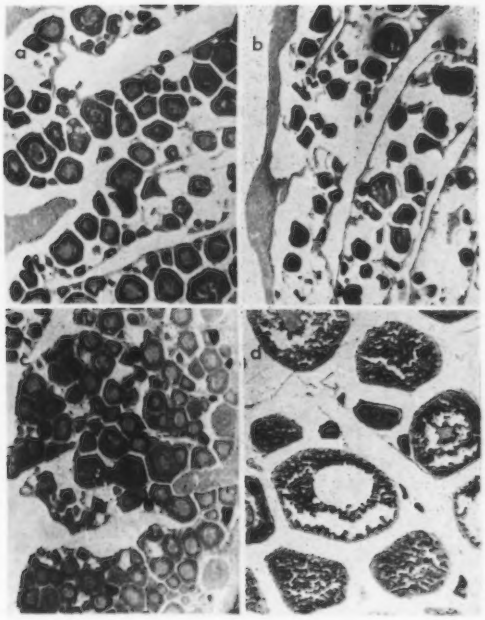

FIG. 2. Ovarian sections from *M. punctatum* in collections: (a) Biological Station FRB St. John's, No. 3224, 79-mm SL, 43°25′N, 51°11′W, March 19, 1955; (b) Biological Station FRB St. John's, No. 6371, 80-mm SL, 42°55′N, 50°48′W, May 31, 1964; (c) Biological Station FRB St. John's, No. 2430, 94-mm SL, 46°36′N, 59°13′W, November 1, 1952; (d) U.S. Nat. Mus. No. 199163, 77-mm SL, 38°57′N, 66°42′W, January 14, 1959. X200.

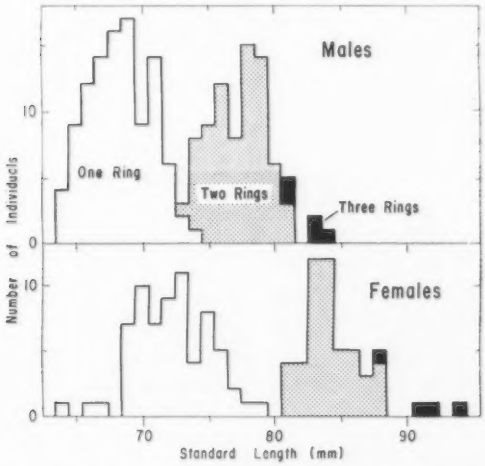

FIG. 3. Length frequency diagram for *M. punctatum* taken by M/V *Brandal* at 50°30′N, 49°30′W, July 12, 1968, showing number of individuals having one, two, or three outer hyaline rings on otoliths.

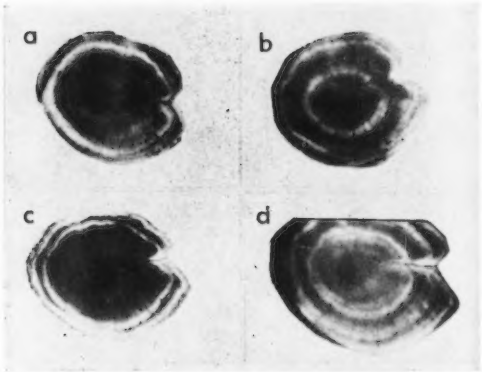

FIG. 4. Otoliths from *M. punctatum* caught by M/V *Brandal* at 50°30′N, 49°30′W, July 12, 1968: (a) from a male, 68-mm SL, showing one outer ring; (b) from a female, 70-mm SL, showing both an inner and one outer ring; (c) from a female, 81-mm SL, showing two outer rings; (d) from a male, 75-mm SL, showing an inner and two outer rings. X16.

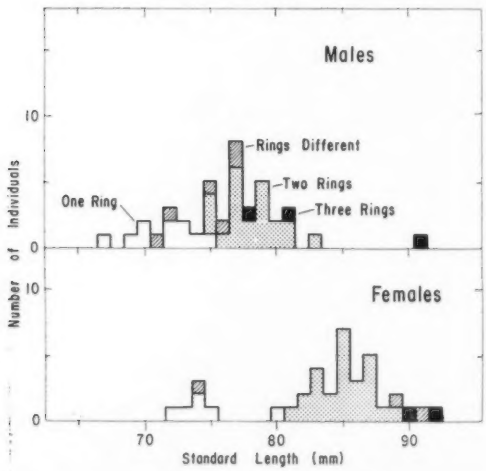

FIG. 5. Length frequency diagram for *M. punctatum* taken by *E. E. Prince*, tow 15, NE of Magdalen Islands, August 1968. Individuals having one outer hyaline ring on otolith and one eroded scale edge (or ring) are labelled One Ring; similarly for Two Rings and Three Rings. Those not corresponding are labelled Rings Different.

Scale and Bone Peculiarities

The large, cycloid scales of adult *M. punctatum* from the northwest Atlantic indicate an irregular growth pattern. The outer circuli are intricate, irregular, and often discontinuous, while the first 35–55 circuli are intact and regularly spaced. Subsequent to erosion at the anterior and anterior–lateral scale edge, several partial circuli fill in the irregularities of the former boundary. Eventually one circulus, and those forming after, surrounds the anterior and lateral fields until growth again ceases (followed by another period of erosion). By simple dissection with a needle and forceps, that part of the scale representing growth after erosion can be peeled away from the overlapping previous growth increment.

Each time an eroded edge appears, a "check" may be said to occur. Occasionally some scales carry a "true annulus" mark, similar to that described by Van Oosten (1928). When present, this annulus is found only within the area delimited by the first eroded scale edge. Scale characters are illustrated in Fig. 6.

Routine clearing and staining of four *M. punctatum*, caught in the Gulf of St. Lawrence during August, revealed that all specimens possessed partially decalcified subopercular bones.

The irregular growth pattern of the scales and bone decalcification are suggestive of a fish in a stress situation, perhaps a result of marginal living conditions.

Length Distributions and Aging

Lengths — All specimens, numbering over 1000, of *M. punctatum* captured north of the Grand Banks are over 60-mm SL with one exception at 46-mm SL. Juveniles (without luminous caudal plates), 30–45-mm SL, are found sporadically off the continental margin from Flemish Cap south to Cape Hatteras. A few samples contain both juvenile and adult individuals, but not in a graduated series of sizes (e.g. 1 juvenile and 300 large adults). Postlarvae of *M. punctatum* were not captured in any sample.

The paucity of young *M. punctatum* in the northwest Atlantic indicates at least some recruitment from elsewhere. If this species can be aged, then the period of time taken to reach this area can be determined.

Otoliths — The length frequency distributions are plotted with reference to hyaline otolith rings for a combined sample of *M. punctatum* (Fig. 3). Sample otoliths are shown in Fig. 4.

A particular number of outer hyaline otolith rings associates with a particular length mode (mm, SL). For males, the mode 69 (Range: 64–74) corresponds to 1 ring and the mode 78 (Range: 73–81) to 2 rings. Five males (81–84) and four females (88–94) have otoliths with 3 rings.

Scales and otoliths — Scale "checks", otolith rings, and lengths are related in Fig. 5 for a sample of 78 *M. punctatum*. The numbers of otolith rings and scale "checks" for 70 specimens are equal and correlate well with the lengths. One fish has unreadable otoliths and the other seven have more otolith rings than scale "checks." The latter individuals exhibit either a region of narrowed circuli or a true "annulus" on their scales within the area delimited by the first "check."

These data demonstrate that relative aging of this species can be accomplished but, as yet, data are insufficient for absolute aging.

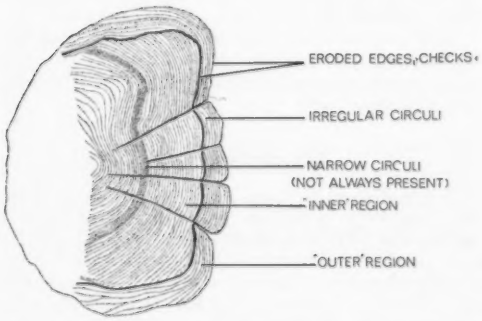

FIG. 6. A typical *M. punctatum* scale, taken just posterior to the pectoral fin. The inner region, while in a majority of cases displaying even growth, occasionally possesses narrowed circuli and even a true annulus.

Discussion

The populations of *M. punctatum* in the northwest Atlantic appear to be nonreproducing. No postlarvae and relatively few juveniles are present. Females have ovaries with only small oocytes. Growth is in irregular cycles and the species grows much larger in the northwest Atlantic than in the Mediterranean, indicative of possible vegetative growth. Sexual caudal luminous plates average less in number in northwest Atlantic populations than in Gibraltar or Mediterranean populations–a symptom perhaps of nonfunctioning gonads and low hormone levels.

This conclusion of expatriation is drawn from the data, despite incomplete sampling from November

to April. It may be justified, based on the following premises.

Within the family Myctophidae, spawning occurs over a protracted time period, usually from winter on into summer. Myctophid postlarvae of different species come to peak abundance in late spring and early summer, although they occur in varying numbers throughout most of the year (Taning 1918). In recent years Isaacs–Kidd Midwater Trawls with fine mesh liners have been used extensively in the northwest Atlantic; yet, to date, no *M. punctatum* postlarvae have been recorded. It is doubtful that this is sampling error.

In two North Pacific *Myctophum* species (Odate and Ogawa 1961), in the two North Atlantic *Lobianchia* species (O'Day and Nafpaktitis 1967), and in many eastern Atlantic and Mediterranean lanternfishes, including *M. punctatum* (Taning 1918), there are large, yolky eggs (0.40–0.50 mm) present in the ovaries of reproducing females through most, if not all, of the year. *M. punctatum* from the northwest Atlantic do not possess such large eggs.

Parallel cases of expatriation exist in the northwest Atlantic. O'Day and Nafpaktitis (1967) consider the two species of *Lobianchia* to be vegetative in most of the western North Atlantic. The expatriated individuals have only small, undeveloped eggs at any time of the year, while individuals in the spawning areas consistently possess large, yolky eggs. Nafpaktitis (1968) suspects that several species of *Diaphus* are also expatriated in the western North Atlantic.

Halliday (1970), whose observations are based on collections totalling over 45,000 *Benthosema glaciale*, points to about 30 females with large, yolky eggs in January–February and to two postlarvae caught in July as evidence of local spawning off Nova Scotia. However, Holt and Byrne (1911), Taning (1918), and Legendre (1934) caught large numbers of *Benthosema* postlarvae in the eastern Atlantic and Mediterranean. Furthermore, Taning found eggs of 0.25–0.50 mm in February, June, and September females with the number of fish approaching a gravid state the lowest in February. *B. glaciale* populations in the northwest Atlantic are remarkably deficient in displaying evidence of spawning.

Expatriation is a common phenomenon in the northwest Atlantic. Huntsman (1919) reports on a chaetognath which grows large without maturing in Arctic waters. Ekman (1953) cites numerous examples of pelagic zooplankters which can become expatriated. Grainger (1963: p. 83) says of *Calanus finmarchius* off Labrador: "At the northern extremities of its range the species is represented only by old individuals which evidently are able to survive but not to breed."

Huge reproducing populations of *M. punctatum* exist in the eastern North Atlantic. In July 1965, two vessels, the M/V *Brandal* and the hydrographic vessel *Fort Frances*, found a sharp transition of oceanic water masses east of Flemish Cap. This phenomenon is well documented in recent years, but a debate exists as to the origin of the warm, saline eastern water mass. In this case, the faunal components were definitely of eastern Atlantic origin, for example, *Electrona rissoi*, *Gonostoma denudatum*, and *Argyropelecus hemigymnus*. Also present were *M. punctatum* juveniles (301 juveniles, 30–47-mm SL, and 3 adults, in eight tows). The impinging Labrador waters also contained *M. punctatum*, but almost exclusively adults (429 adults over 64-mm SL and 1 juvenile in eight tows). The mesopelagic fish species characteristic of the eastern Atlantic were absent in the cold water. These data are consistent with the pelagic regions of Backus et al. (1970) as delineated by faunal transects (Backus et al. 1965). It is possible that a clockwise eastern Atlantic gyre (Worthington 1962) sweeps mesopelagic fishes westward. Although C. R. Mann (personal communication) warns that Worthington's "two gyre" theory of North Atlantic circulation is not established as fact, these data do show the close apposition of eastern and western faunas.

There appears to be little interchange of faunal elements off Flemish Cap, but, farther north, conceivably young *M. punctatum* are spun off westward. Documentation in the literature reveals a continuous distribution of *M. punctatum* across the northernmost Atlantic (Lutken 1892; Brauer 1906; Saemundsson 1949; Bolin 1959). Grainger (1963) cites an example of east west drift for populations of *Calanus glacialis* progressing from east of Greenland in June to the eastern Labrador Sea and Hudson Strait by July.

Extensive mid-North Atlantic sampling and the development of reliable aging techniques for *M. punctatum* are essential before a better understanding can be gained.

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Mercury Concentration in Relation to Size in Several Species of Freshwater Fishes from Manitoba and Northwestern Ontario

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Scott, D. P., and F. A. J. Armstrong. 1972. Mercury concentration in relation to size in several species of freshwater fishes from Manitoba and northwestern Ontario. J. Fish. Res. Bd. Canada 29: 1685–1690.

Statistical analysis of 53 samples of 11 species of fishes from a number of areas of Manitoba and northwestern Ontario indicated that in general there was a positive correlation between mercury concentration and length. There also appeared to be a more variable positive relation between mercury concentration and fish condition (fatness). It was possible to predict, for 31 of the 53 samples, the range of lengths within which there was a 95% probability of all fish containing less than 0.5 ppm mercury. However, within species the relation between mercury concentration and length was not consistent. The results show that, for certain of the populations closed to commercial fishing because of mercury contamination, selection (by fishing technique or otherwise) of certain sizes should provide fish of acceptably low mercury concentration.

Scott, D. P., and F. A. J. Armstrong. 1972. Mercury concentration in relation to size in several species of freshwater fishes from Manitoba and Northwestern Ontario. J. Fish. Res. Bd. Canada 29: 1685–1690.

L'analyse statistique de 53 échantillons prélévés sur 11 espèces de poissons habitant diverses régions du Manitoba et du nord-ouest de l'Ontario démontre qu'il y a généralement une corrélation positive entre la teneur en mercure et la longueur du poisson. Il semble y avoir une corrélation également positive, mais plus variable, entre la teneur en Hg et l'indice d'embonpoint. Dans 31 des 53 échantillons, il est possible de prédire l'intervalle de longueurs dans la limite desquelles il y a probabilité de 95% que tous les individus contiendront moins de 0.5 ppm de Hg. Ces résultats démontrent que, chez quelques-unes des populations où la pêche commerciale est interdite à cause de la contamination au Hg, la sélection (par des techniques de pêche ou autrement) de tailles particulières permettrait de récolter des poissons à teneur en Hg assez basse pour être acceptable.

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Some commercial fisheries in Canada have been closed because the fish have been found to contain unacceptably high concentrations of mercury. The maximum level of this element at which fish may legally be marketed has been set at 0.5 ppm (mg/kg wet weight).

The statistical analyses presented here were undertaken in order to investigate the relation between mercury concentration and fish size, with the aim of discovering whether, in any of the populations studied, there might be positive correlations strong enough to establish size limits within which safe mercury concentrations should be found. If this were so, selection for size when fishing or before marketing might allow safe operation of some presently closed fisheries.

Answers for the following questions were required.

(1) Are there, in general, firm relations between mercury concentrations and fish sizes, and what data transformations are needed to ensure linearity and homoscedasticity?

(2) Are the relations different from species to species and from area to area, requiring separate investigations for each commercial population?

(3) Are the relations sufficiently strong, within populations, to allow reasonably accurate predictions?

(4) Do there exist size ranges within which at least 95% of individual fish have less than 0.5 ppm mercury, and are these ranges commercially practical?

Materials and Methods

Samples of approximately 20 specimens each of 11 species of fish from a number of fishing areas were obtained by gill netting; the largest available size range of

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individuals was collected. Fork lengths and total weights were recorded. Mercury in the white muscle was determined by the method of Armstrong and Uthe (1971), the means of duplicate or triplicate analyses being reported.

Statistical analyses were performed on the data as follows:

(1) Within-sample regressions of weight on length, mercury on length, mercury on weight, and mercury on length and condition. Condition is defined as the difference, positive or negative, between actual $\log_e$ weight and expected $\log_e$ weight predicted from the double-log weight–length relation for the particular

TABLE 1. Weight/length and mercury/length/condition relations in various species of fish from several areas, and ranges of fork length calculated for acceptable mercury content. All computations on natural logs of data. Samples in order of increasing adjusted group means of mercury concentration within species. $X_1 = \log_e$ (fork length, *cm*); $X_2 = \log_e$ (weight, *g*); $X_3 = \log_e$ (mercury content, *ppm*); $X_4 = \log_e$ (condition factor) $= \log_e (X_2/E(X_2))$. Significance by superscript: $^0 = P < 0.9$; $^1 \leqq 0.9 \leqq P < 0.99$; $^2 = 0.99 \leqq P$ 0.999; and $^3 = 0.999 \leqq P$.

				Regression of X_2 *on* X_1			Regression of X_3 *on* X_1 and X_4						
Species	Areas	Province	N	$\hat{a}$	$\hat{b}_{21}$	$\hat{r}^2$	$\hat{a}$	$\hat{b}_{31.4}$	$\hat{b}_{34.1}$	$\hat{R}^2$	$ad\ \overline{X}_3$ (*ln*)	$ad\ \overline{X}_3$ (*ppm*)	Fork length (*cm*) acceptable range
White sucker	Eating Pt., L. Winnipeg	Man.	20	−1.977	2.389^3	0.833	−11.967	2.516^2	0.568^0	0.467	−3.111	0.045	<61.6
(*Catostomus*	Mouth of Red R.	Man.	20	−4.233	3.012^3	0.913	−13.704	3.253^3	1.324^2	0.867	−2.253	0.105	<43.9
commersoni)	Hnausa, L. Winnipeg	Man.	39	−4.686	3.150^3	0.932	−12.450	2.959^3	0.176^0	0.440	−2.034	0.131	<41.0
	Clay L.	Ont.	20	−3.051	2.701^3	0.849	−3.558	1.326^1	0.956^1	0.331	+1.109	3.031	None
Burbot	Long Pt., L. Winnipeg	Man.	20	−4.475	2.939^3	0.958	−14.057	3.096^3	-0.621^0	0.608	−1.925	0.146	<58.9
(*Lota lota*)	Eating Pt., L. Winnipeg	Man.	20	−1.459	2.201^3	0.679	−5.732	1.036^1	0.819^1	0.419	−1.672	0.188	<71.4
	Mouth of Red R.	Man.	20	−4.250	2.858^3	0.872	−8.245	1.883^2	0.381^0	0.440	−0.867	0.420	<37.8
	Elk Is., L. Winnipeg	Man.	19	−4.606	2.969^3	0.921	−6.247	1.431^3	0.477^0	0.540	−0.640	0.527	<33.4
Yellow perch	Big Black R., L. Winnipeg	Man.	19	−3.417	2.797^3	0.856	−11.060	2.983^2	0.608^0	0.364	−1.627	0.197	<24.8
(*Perca flavescens*)	Hnausa, L. Winnipeg	Man.	20	−1.202	2.026^2	0.432	−0.874	0.237^0	2.133^0	0.032	−0.631	0.532	No solution
	Victoria Beach., L. Winnipeg	Man.	20	−1.113	2.028^2	0.403	−7.278	2.160^0	-0.645^0	0.179	−0.449	0.638	No solution
Sauger	Black Bear Is., L. Winnipeg	Man.	20	−0.621	3.482^3	0.901	−0.651	-0.120^0	0.575^0	0.020	−1.064	0.345	No solution
(*Stizostedion*	Hnausa, L. Winnipeg	Man.	20	−5.190	3.183^3	0.768	−2.951	0.606^0	0.584^0	0.119	−0.869	0.419	No solution
canadense)													
Walleye	Cormorant L.	Man.	20	−4.509	3.006^3	0.866	−10.532	2.466^2	-0.084^0	0.426	−1.400	0.247	<45.4
(*Stizostedion*	North. L. St. Martin	Man.	23	1.675	1.326^3	0.447	+0.383	-0.451^0	-1.253^1	0.138	−1.286	0.276	34.9–45.4
vitreum vitreum)	Eating Pt. '71, L. Winnipeg	Man.	20	−3.303	2.711^3	0.937	−5.946	1.284^1	1.289^0	0.305	−1.191	0.304	<42.1
	Long Pt., L. Winnipeg	Man.	20	−2.566	1.930^3	0.580	+1.000	-0.571^0	0.777^1	0.184	−1.113	0.329	No solution
	Sturgeon Bay, L. Winnipeg	Man.	20	−3.644	2.790^3	0.821	−2.876	0.491^0	-0.749^0	0.093	−1.060	0.346	No solution
	Eating Pt. '70, L. Winnipeg	Man.	20	−3.003	2.650^3	0.594	−7.337	1.702^2	0.901^2	0.593	−1.037	0.355	<35.7
	Cliff L.	Ont.	20	−4.497	3.048^3	0.950	−8.405	2.042^3	1.190^1	0.702	−0.845	0.430	<33.4
	Cedar L.	Man.	20	−6.629	3.590^3	0.901	−7.605	1.826^3	-0.207^0	0.591	−0.842	0.431	<39.5
	Sask. R. at The Pas	Man.	20	−2.052	2.343^3	0.661	−2.017	0.408^0	0.703^0	0.064	−0.508	0.602	No solution
	Grassy L.	Ont.	19	−5.467	3.277^3	0.949	−5.168	1.593^1	-0.223^0	0.266	+0.733	2.081	<1.83
	Ball L.	Ont.	20	−4.685	3.086^3	0.945	−2.040	0.810^0	-0.616^0	0.059	+0.960	2.612	None
	Separation L.	Ont.	20	−5.541	3.299^3	0.961	−2.232	0.893^1	1.417^1	0.390	+1.074	2.927	None
	Clay L.	Ont.	24	−4.507	3.050^3	0.923	−0.481	0.680^0	-1.463^0	0.089	+2.037	7.668	None
Northern pike	Moose L.	Man.	20	−6.713	3.500^3	0.889	−5.601	0.793^0	-0.427^0	0.134	−2.470	0.085	0–124.2
(*Esox lucius*)	Hnausa, L. Winnipeg	Man.	20	−5.413	3.134^3	0.804	−4.605	0.788^0	0.585^0	0.191	−1.573	0.207	1.4–72.3
	Cormorant L.	Man.	21	−6.331	3.401^3	0.890	−10.726	2.359^2	0.192^0	0.463	−1.409	0.249	<57.2
	Saskatchewan R. at The Pas	Man.	24	−5.377	3.164^3	0.858	−14.319	3.296^2	0.739^0	0.551	−1.299	0.273	<46.9
	Sturgeon Bay, L. Winnipeg	Man.	20	−4.850	3.014^3	0.947	−5.364	1.040^2	0.152^0	0.381	−1.256	0.285	<62.3
	Victoria Beach, L. Winnipeg	Man.	20	−5.262	3.124^3	0.956	−6.541	1.343^1	-0.301^0	0.282	−1.237	0.290	<52.2
	North. L. St. Martin	Man.	20	−0.725	1.921^2	0.320	−0.951	-0.030^0	0.071^0	0.003	−1.069	0.343	No solution
	Dryberry L.	Ont.	21	−2.339	2.416^3	0.655	−10.350	2.385^1	0.668^0	0.350	−0.928	0.395	<33.6
	Eating Pt., L. Winnipeg	Man.	20	−7.369	3.622^3	0.924	−4.449	0.893^0	-0.747^0	0.176	−0.922	0.398	No solution
	Cedar L.	Man.	20	−6.851	3.476^3	0.899	−7.498	1.690^1	0.750^0	0.330	−0.822	0.440	<43.7
	Red R. at Selkirk	Man.	20	−5.163	3.063^3	0.922	−5.239	1.124^1	-0.100^0	0.229	−0.798	0.450	<39.6
	Tetu L.	Man.	20	−6.460	3.411^3	0.897	−5.206	1.565^1	-0.175^0	0.165	+0.975	2.651	None
	Grassy L.	Ont.	20	−4.331	2.846^3	0.928	−5.659	1.735^2	-0.638^0	0.380	+1.195	3.304	<3.6
	Ball L.	Ont.	20	−3.767	2.711^3	0.773	−7.666	2.269^2	-1.993^2	0.545	+1.296	3.655	None
	Separation L.	Ont.	20	−8.003	3.752^3	0.943	−3.925	1.348^1	-0.783^0	0.231	+1.399	4.051	None
	Clay L.	Ont.	25	−5.019	3.019^3	0.805	−2.810	1.264^2	-0.279^0	0.287	+2.184	8.873	None
Sheepshead	Elk Is., L. Winnipeg	Man.	20	−4.424	3.157^3	0.888	−8.303	2.062^1	0.682^0	0.181	−1.662	0.190	<28.6
(*Aplodinotus*	Mouth of Red R.	Man.	20	−1.613	2.290^3	0.722	−5.693	1.277^0	0.229^0	0.083	−1.581	0.206	4.8–30.4
grunniens)													
Lake whitefish	Kakagi L.	Ont.	20	−3.016	2.617^2	0.444	−11.124	2.225^1	0.434^0	0.270	−2.985	0.051	<68.3
(*Coregonus*	Sydney L.	Ont.	18	−3.099	2.665^3	0.732	−6.705	1.229^0	-0.643^0	0.152	−2.210	0.110	2.2–64.0
clupeaformis)	Clay L.	Ont.	20	−2.600	2.542^3	0.954	+0.691	0.032^0	2.166^0	0.104	+0.808	2.243	No solution
Tullibee	Victoria Beach, L. Winnipeg	Man.	20	−4.372	3.086^3	0.847	+0.128	-0.654^0	-1.297^1	0.190	−1.927	0.146	16.5–61.2
(*Coregonus*	Hnausa, L. Winnipeg	Man.	20	−3.486	2.769^3	0.712	+0.391	-0.696^0	-0.780^0	0.122	−1.797	0.166	16.3–62.8
artedii)	Mouth of Red R.	Man.	19	−6.706	3.729^3	0.945	−6.434	1.509^2	-0.843^0	0.443	−1.693	0.184	<31.2
	Elk Is., L. Winnipeg	Man.	20	−5.126	3.260^3	0.902	+2.155	-1.207^1	-0.001^0	0.270	−1.639	0.194	>15.6
Lake trout	Kakagi L.	Ont.	20	−6.666	3.589^3	0.963	−10.008	2.143^3	0.577^0	0.521	−1.369	0.254	<57.0
(*Salvelinus*													
namaycush)													
Goldeye	Saskatchewan R. at The Pas	Man.	20	−4.013	2.862^3	0.656	−7.534	2.118^0	-0.134^0	0.079	−0.407	0.666	No solution
(*Hiodon alosoides*)													

sample. Computations were carried out on both untransformed data and on natural-log transformed variables. The latter proved to be appropriate for both linearizing the relations and uncoupling means and variances. The method used to confirm this is to be the subject of a later paper.

(2) From the within-sample relations, predictions were attempted to show the range of sizes at which 95% of individuals would have less than 0.5 ppm mercury content. The method used is outlined in Kenney and Keeping (1951) and consists essentially of equating the appropriate confidence limits (i.e. upper 95%) with the desired 0.5 ppm value and solving the resultant quadratic equations. It should be noted that such predictions can be made regardless of the significance of the particular sample regression; the limits take sample variances and covariances into account.

(3) Analyses of simple and multiple covariance (after Mood 1950) were used to determine whether there were significant between-area differences in the relations within species. Between-species differences were so obvious that comparisons between species or within areas were not pertinent. Standard tests were made for the statistical differences between adjusted group means ($ad\overline{X}_j$), simple regression coefficients ($\hat{b}_{jk}$), partial regression coefficients ($\hat{b}_{jk \cdot i}$), the weighted mean partial regression coefficients for each species and zero ($\hat{b}_{jk \cdot w} = 0$), and the weighted mean partial regression coefficients for all samples lumped together and zero. Bartlett's (1937) test was used to test for within-species homogeneity of residual variance.

Results

Although not presented here, results of separate comparisons of simple correlations of mercury concentration on length and of mercury concentration on weight showed that there was little to choose between the two where both were significant. Length was therefore chosen as the basic measure since it is less likely to be subject to major day-to-day fluctuations; weight is highly influenced by feeding. Table 1 shows the weight/length and mercury/length/condition relationships for the samples, and ranges of length calculated for acceptable mercury concentration. Table 2 presents the results of analyses of simple and multiple covariance for between-sample, within-species comparisons of

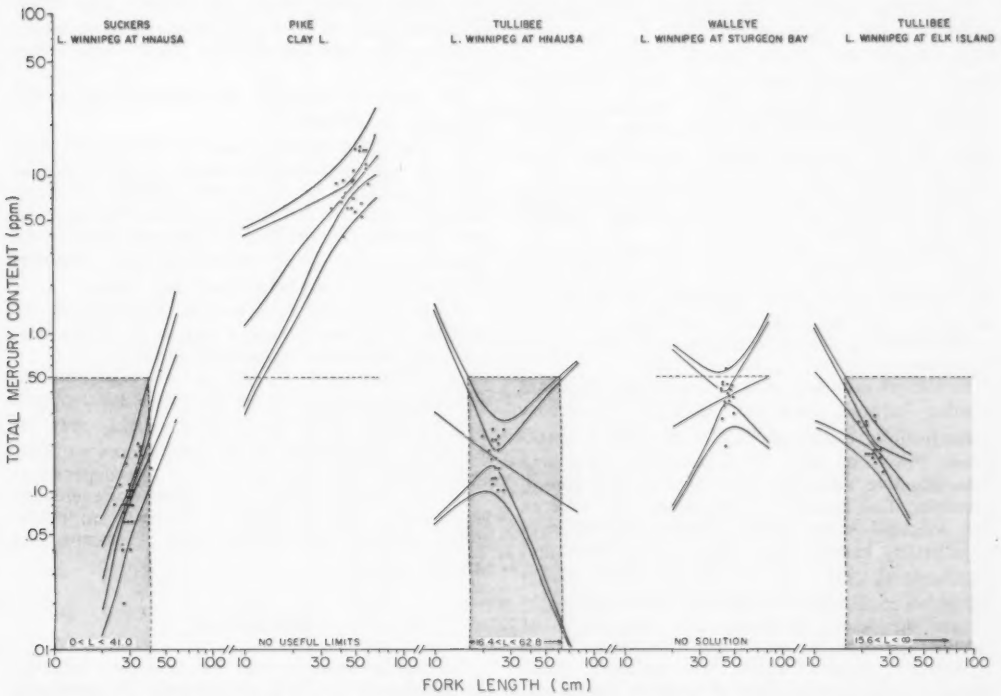

FIG. 1. Confidence limits for selected regressions of $\log_e$ mercury content on $\log_e$ length. Inner limits are 95% confidence limits on the regressions; outer limits are 95% limits on individuals.

adjusted group means, simple and partial regression coefficients, and homogeneity of residual variance.

Several points are immediately obvious from the tables. Within species, the relation between mercury concentration and length was not consistent. Most important from a practical viewpoint are the very large differences between the various samples. These range from complete lack of significance to strong correlations in the mercury relations. Figure 1 presents five examples:

(1) Strong positive correlation, low average mercury content: Yellow sucker (*Catostomus commersoni*); Hnausa, Lake Winnipeg; length limit < 41.0 cm.

(2) Strong positive correlation, high average mercury content: Northern pike (*Esox lucius*); Clay Lake; limit too small to be practical (<0.2 cm)

(3) Weak or no correlation, low average mercury content: tullibee (*Coregonus artedii*); Hnausa, Lake Winnipeg; length limits 16.4–62.5 cm.

(4) Weak or no correlation, high average mercury content: walleye (*Stizostedion vitreum vitreum*); Sturgeon Bay, Lake Winnipeg; no solution-complex roots.

(5) Strong negative correlation, low average mercury content: tullibee; Elk Island, Lake Winnipeg; length limit greater than 15.6 cm.

Some populations, particularly those from the Wabigoon River system (Clay, Separation, Ball, and Grassy lakes) and Winnipeg River (Tetu L.), show that no practical length limit exists; these populations are not usable commercially.

There appears to be no relation between average population mercury concentration and strength of correlation in the mercury concentration on length or condition relations. As an example, the average coefficient of determination (unweighted) of the five pike groups with the highest mercury concentration is almost identical with that of the five lowest, i.e. 0.322 versus 0.344.

Of the 53 samples, only 10 show any significant relation between condition of fish and mercury concentration based on partial regression coefficients. Seven of these show positive slopes and three negative, although no consistency is apparent. However, if all groups are considered (see Table 2), the weighted mean partial regression coefficient for mercury content on condition is positive and significant at $.975 < P < .99$. Of the 53 partial regression coefficients for mercury content on length, 33 are significant; of these, only the sample of tullibee for Elk Island, Lake Winnipeg, shows a negative slope. Overall, the weighted mean partial regression coefficient of mercury content on length is strongly positive and significant at $.999 < P$. Some doubt arises about the validity of the Tullibee (Elk Island) result since the other three groups of this species show either nonsignificant negative slopes or a significant positive coefficient (mouth of Red River). The other two species sampled at Elk Island (Burbot (*Lota lota*) and Sheepshead (*Aplodinotus grunniens*) both show significant positive slopes. In six of the nine species examined, the adjusted group means of mercury content differ significantly between sampling areas. Within-species differences in regression slopes (Table 2), however, are much less strong, only five species showing moderate significance of mercury concentration on length; two species show significance of differences of mercury concentration on condition. Six species shew significant departure from zero of the weighted mean regression coefficient of mercury concentration on length, and four show departures from zero for mercury concentration on condition. The analyses of the weight–length relations are presented to show the necessity of using a within-sample measure of condition.

Differences in residual variance are present in both weight on length and mercury concentration on length or condition relations, particularly in the two major species, pike and walleye. The other differences are so great, however, that it seems unlikely that nonhomogeneity would negate the previous results.

The questions posed in the introduction can be answered as follows:

(1) There is generally a positive relation between mercury concentration and length of fish which is slightly modified by a variable relation between mercury concentration and condition. The logarithmic transformation of the variables was found to be appropriate for both linearizing and ensuring reasonable homoscedasticity of the data.

(2) The relations vary greatly from sample to sample. One must conclude that each population must be treated as a separate entity.

(3) For this set of samples, the relations are variable, some being useful for predictions, others not. In many cases, the latter condition may be due to the short range of the independent variable as compared with the variance of the dependent.

(4) Of the 53 samples, 31 show commercially feasible size ranges, 10 show definitely no possibilities, 11 show no solution, and 1 indicates too short a range.

Discussion

General conclusions may be drawn as follows: (1) the sample size of approximately 20 specimens is somewhat too small to allow for good prediction; (2) a wider range of sizes would have been desirable

TABLE 2. Analyses of covariance and multiple covariance and tests for homogeneity of residual variance for weight–length and mercury–length–condition relations in various species of fishes from several areas. Variables and probability levels as in Table 1.

	Regression of X_2 *on* X_1						Regression of X_3 *on* X_1 and X_4											
	$a\overline{dX}_{2i}$ equal		$\hat{b}_{21i}$ equal		$\hat{s}^2_{21i}$ equal		$a\overline{dX}_{3i}$ equal		$\hat{b}_{31.4i}$ equal		$\hat{b}_{31.4w} = 0$		$\hat{b}_{34.1i}$ equal		$\hat{b}_{34.1w} = 0$		$\hat{s}^2_{3.14i}$ equal	
Species	df	F	df	F	df	χ^2/df	df	F	df	F	df	F	df	F	df	F	df	χ^2/df
Sucker	3;94	0.970[0]	3;91	2.367[1]	3	3.202[1]	3;93	403.4[3]	3;87	2.268[1]	1;87	100.5[3]	3;87	0.840[0]	1;87	9.246[2]	3	1.089[0]
Burbot	3;74	3.102[1]	3;71	1.775[0]	3	3.146[1]	3;73	63.72[3]	3;67	3.075[1]	1;67	59.15[3]	3;67	0.900[0]	1;67	4.243[1]	3	1.504[0]
Perch	2;55	13.56[3]	2;53	1.262[0]	2	0.381[0]	2;54	48.23[3]	2;50	2.769[1]	1;50	9.454[2]	2;50	0.767[0]	1;50	0.074[0]	2	1.970[0]
Sauger	1;37	0.085[0]	1;36	0.382[0]	1	0.508[0]	1;36	3.524[1]	1;34	0.240[0]	1;34	0.047[0]	1;34	0.000[0]	1;34	1.295[0]	1	5.900[1]
Walleye	12;252	7.616[3]	12;240	3.129[3]	12	5.518[3]	12;251	245.6[3]	12;227	1.355[0]	1;227	35.35[3]	12;227	1.792[1]	1;227	5.671[1]	12	5.426[3]
Pike	15;314	6.487[3]	15;299	1.844[1]	15	4.086[3]	15;313	285.3[3]	15;283	1.988[1]	1;283	115.8[3]	15;283	2.185[2]	1;283	0.819[0]	15	4.261[3]
Sheepshead	1;37	0.417[0]	1;36	4.190[1]	1	0.206[0]	1;36	0.590[0]	1;34	0.249[0]	1;34	4.854[1]	1;34	0.132[0]	1;34	0.484[0]	1	0.608[0]
Whitefish	2;54	4.485[1]	2;52	0.029[0]	2	1.736[0]	2;53	139.5[3]	2;49	0.360[0]	1;49	0.080[0]	2;49	1.451[0]	1;49	2.649[0]	2	2.347[1]
Tullibee	3;75	16.47[3]	3;72	1.942[0]	3	1.040[0]	3;74	2.135[0]	3;67	3.509[1]	1;67	0.004[0]	3;67	0.739[0]	1;67	8.291[2]	3	4.216[2]
Total											1;932	254.8[3]			1;932	6.564[1]		
											weighted mean $\hat{b}_{31.4w} = 1.442$				weighted mean $\hat{b}_{34.1w} = 0.219$			

in most of the samples, since the predicted values are well outside the sample range, and (3) it seems likely that many of the closed fisheries could be restored to limited production if selective fishing were carried out.

With respect to the last conclusion, pike in particular are known to be able to withstand considerable fishing pressure, since the overall biomass may increase though the average size of individuals decreases (Lawler 1961). Thus, it seems unlikely that there would be appreciable damage to most pike populations if the average size utilized were small. If some method of fishing were used which permitted undamaged return of the larger fish, these would constitute the spawning population without resort to any decrease in average age or size at reproduction. It would seem to be an excellent way to protect the population's spawning potential unless, of course, it should turn out that mercury reduces fecundity. Whether other species could stand the same kind of selective fishing is unknown.

The acceptability of smaller fish to the commercial fishery is also unknown; certainly there would be greater handling costs for a given total poundage.

It might be well to note that there are several specific values of the partial regression coefficient $\hat{b}_{31.4}$ that have particular meanings. These are:

(1) $\hat{b}_{31.4} = -1/\hat{b}_{21}$. If there is a particular mercury content at the beginning of a growth period, and no new mercury is absorbed, then dilution alone by growth will result in a slope approximately the negative reciprocal of the weight–length relation slope coefficient. A value of $\hat{b}_{31.4}$ more negative than this probably indicates excretion of mercury.

(2) $\hat{b}_{31.4} = 0.0$. This value does not mean that there is no relation between size and total mercury content; rather, it indicates that there is no change in mercury concentration with size. In fact, the fish must absorb mercury at a rate which just matches their growth in weight to produce this value. Values of $\hat{b}_{31.4}$ larger than 0.0 obviously indicate absorption of mercury at a greater rate than the combined effects of excretion and growth.

In addition, the inner 95% confidence limits shown in Fig. 1 for the regressions could be used to predict lengths at which 95% of sample means (of say, 20 fish), rather than 95% of individual fish, would be ≤ 0.5 ppm of mercury. The difference between such values and those from the predictions for individuals depends on sample correlation; very high correlation would bring the limits close together, low correlation far apart. In the latter case, the predicted length becomes dangerous to use since some of the fish caught might have very high (>5.0 ppm) mercury concentrations, and still give a sample mean of 0.5 ppm (one meal from a 5.0 ppm fish is equivalent to at least 10 meals from a 0.5 ppm fish). We feel that the risk in predicting from the limits of means is potentially too great to be acceptable, even if it resulted in some fisheries remaining closed, whereas predictions based on distributions of individual values is not subject to such a danger. It is obvious that continual monitoring of any attempted commercial operation would be essential.

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Effects of Various Metals on Survival, Growth, Reproduction, and Metabolism of *Daphnia magna*

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The toxicities of various metals to *Daphnia magna* were evaluated on the basis of a 48-hr 50% lethal concentration (LC50) a 3-week LC50, and a 16% decrease in the number of young born (reproductive impairment). The 3-week 16% reproductive impairment concentrations (in micrograms per liter) for the metal ions tested were: Na(I), 680,000; Ca(II), 116,000; Mg(II), 82,000; K(I), 53,000; Sr(II), 42,000; Ba(II), 5800; Fe(III), 4380; Mn(II), 4100; As(V), 520; Sn(II), 350; Cr(III), 330; Al(III), 320; Zn(II), 70; Au(III), 60; Ni(II), 30; Pb(II), 30; Cu(II), 22; Pt(IV), 14; Co(II), 10; Hg(II), 3.4; and Cd(II), 0.17. At metal concentrations permitting survival but impairing reproduction, daphnids weighed less than control animals. Amounts of total protein and glutamic oxalacetic transaminase activity varied with the different metals. The negative logarithm of the solubility product constant (pK_{sp}) of the metal sulfides, electronegativity, and the logarithm of the equilibrium constant (log K_{eq}) of the metal–ATP complex were positively correlated with toxicity to *D. magna*. Other physicochemical properties were considered, but no additional correlations were found.

BIESINGER, K. E., AND G. M. CHRISTENSEN. 1972. Effects of various metals on survival, growth, reproduction, and metabolism of *Daphnia magna*. J. Fish. Res. Bd. Canada 29: 1691–1700.

Les auteurs évaluent la toxicité de divers métaux à l'endroit de *Daphnia magna*, en déterminant, après exposition de 48 h et de 3 semaines, la concentration létale au palier de 50% (LC50) et la diminution de 16% du nombre de jeunes à la naissance (abaissement du pouvoir reproducteur). Les concentrations d'ions métalliques produisant un abaissement du pouvoir reproducteur de 16% après 3 semaines (en microgrammes par litre) sont les suivantes: Na(I), 680,000; Ca(II), 116,000; Mg(II), 82,000; K(I), 53,000; Sr(II), 42,000; Ba(II), 5800; Fe(III), 4380; Mn(II), 4100; As(V), 520; Sn(II), 350; Cr(III), 330; Al(III), 320; Zn(II), 70; Au(III), 60; Ni(II), 30; Pb(II), 30; Cu(II), 22; Pt(IV), 14; Co(II), 10; Hg(II), 3.4; et Cd(II), 0.17. Soumises à des concentrations de métaux non létales, mais suffisantes pour abaisser le pouvoir reproducteur, les daphnies pèsent moins que les témoins. Les protéines totales et l'activité de la glutamique-oxalacétique transaminase varient avec les différents métaux. La relation entre la toxicité et certaines propriétés physiques et chimiques permet de prédire la toxicité des métaux chez *Daphnia* à partir de constantes physico-chimiques. Il existe une corrélation positive entre la toxicité à *D. magna* et le logarithme négatif de la constante du produit de solubilité (pK_{sp}) des sulfures métalliques, l'électronégativité, et le logarithme de la constante d'équilibre (log K_{eq}) du complexe métal–ATP. Les autres propriétés physico-chimiques étudiées ne révèlent pas de corrélations additionnelles.

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THE toxic effects of metals to *Daphnia magna* in various natural waters have been considered by numerous investigators on an acute basis. The present study includes acute toxicity values and adds to our knowledge by considering primarily the chronic effects of metals on reproduction, on growth as measured by weight and total protein, and on metabolism as measured by glutamic oxalacetic transaminase (GOT, L-aspartate:2-oxoglutarate aminotransferase) activity. In addition, the relative chronic toxicities of the metals were studied to find possible correlations with certain physicochemical properties of the metals because of the potential usefulness of these correlations.

The advantages of using daphnids as test organisms were noted by Anderson (1944). The importance of daphnids was exemplified in a report by Anderson et al. (1948) in which the authors con-

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cluded that, in sensitivity to toxic substances, *D. magna* was in general representative of other abundant zooplankters. Anderson (1950) compared 64-hr apparent-threshold metal concentrations for daphnids with acute values for fish and concluded that "in general, the *Daphnia* and related forms are more susceptible to cations than are fish."

Studies to correlate toxicity of inorganic chemicals with physical and chemical properties of the chemicals have been made for many years. Danielli and Davis (1951) suggested that the metal ions exert their toxic influence by covalent binding at cell surfaces, and that the difference in electronegativity of the various ions is a toxicity-determining factor. The study of Somers (1959) showed a correlation between toxicity of the metals to *Botrytis fabae* and the electronegativity of the metals. Since the site of action between the metal and the organic ligand appeared to involve nitrogen, sulfur, or other electronegative functional groups, Shaw and Grushkin (1957) and Shaw (1961) related the toxicity for many organisms to metal sulfide solubility and found a positive correlation.

Materials and Methods

Food and Feeding

Daphnia magna from a laboratory clone originally obtained from the University of Michigan were used. They were fed a suspension of food (1 ml/liter) twice weekly for rearing and once weekly for testing. The food suspension was prepared by adding 0.5 g of powdered dried grass and 10 g of enriched trout-fry granules to 250 ml of Lake Superior water and mixing vigorously in a blender for 5 min. The suspension was then strained through #20 bolting cloth. The blender was rinsed with an additional 50 ml of lake water, and the rinse water was added to the suspension. The food thus prepared was stored in a refrigerator and mixed thoroughly each time an aliquot was withdrawn. Unfiltered lake water strained through #20 bolting cloth was used for all rearing and testing; thus, in addition to the food mixture, the daphnids obtained some nutrients from bacteria, algae, and detritus in the water.

Testing Methods

For acute tests, 10 daphnids 12 ± 12 hr old were placed in duplicate test chambers and subjected to test conditions for 2 days (48 hr). Tests were run both with and without food additions as the food changed the toxicity values. Complete immobilization or death was the endpoint.

For chronic studies five daphnids 12 ± 12 hr old were placed in 200 ml of water in a 250-ml beaker. Four beakers (the test chambers) were used with a total of 20 animals for each experimental and control condition for each test. The test chambers were covered with a pane of glass to minimize evaporation, and distributed randomly on a shelf in a constant temperature room (18 ± 1C). Young daphnids were placed in test chambers, transferred into new medium at the beginning of each week with a medicine dropper, and subjected to test conditions for 3 weeks. Survival of the initial animals was noted after 1, 2, and 3 weeks. At the end of 3 weeks the surviving animals were weighed and prepared for protein and GOT analyses. Reproduction was assessed by counting the young produced each week; the young were counted and discarded each time the initial animals were transferred and at the end of each experiment.

A combination of Durotest (Optima FS)[1] and wide-spectrum Grow-lux fluorescent bulbs provided a light intensity of ~115 ft-c at the air–water interface. An automatically controlled 16-hr photoperiod was used.

The number of concentrations tested ranged from 5 to 12 depending on the toxicant and the initial effects observed. Since daphnids had not been previously exposed to metals on a chronic basis, experiments often had to be repeated before appropriate concentrations could be tested. As daphnid response to toxicity was

Table 1. Chemical characteristics (μg/liter except for *p*H) of Lake Superior water.

Item	Mean	Range	No. samples
*p*H[a]	7.74	7.4–8.2	23
Total hardness[b]	45,300	44,000–53,000	54
Alkalinity[b]	42,300	41,000–50,000	54
Chloride[a]	1217	1170–1340	18
Sodium[a]	1130	1090–1190	23
Calcium[a]	13,695	13,000–14,700	23
Magnesium[a]	3123	2940–3590	23
Potassium[a]	534	480–590	23
Strontium[c]	16	12–27	10
Barium[c]	14	8–22	10
Iron[c]	23	2–83	10
Manganese[a]	–	0.2–11.5	23
Chromium[c]	–	2–20	4
Aluminum[c]	–	1–26	5
Zinc[a]	0.78	1–2.7	21
Nickel[a]	<0.5	–	23
Lead[c]	–	7–20	2
Copper[a]	1.51	0.3–3.2	23
Cobalt[a]	<0.5	–	23
Mercury[a]	<0.01	–	5
Cadmium[a]	<0.1	–	23

[a]G. F. Olson (personal communication), National Water Quality Laboratory, Duluth, Minn.
[b]E. N. Leonard (personal communication), National Water Quality Laboratory, Duluth, Minn.
[c]Kopp and Kroner (1969).

[1]Mention of commercial products does not constitute endorsement by the United States Environmental Protection Agency.

often within extremely narrow limits, a geometric series of concentrations was used for obtaining an approximation of toxicity; a linear series of concentrations was often used for delineating reproductive impairment levels. After the concentrations to be tested were determined, three to seven tests were run for each toxicant. The results from all tests for each toxicant concentration were pooled for statistical analysis.

Statistical Evaluations

Results were statistically evaluated with the method of Litchfield and Wilcoxon (1949) for establishing approximations of the 95% confidence limits for survival. The terminology recommended by Sprague (1969), lethal concentration (LC), was used for survival and, as given here, represents an interpolation from three or more partial-effect concentrations. Reproductive effects were analyzed in a similar manner excluding confidence limits, but are given in terms of reproductive impairment by percentage.

Both 50 and 16% reproduction-impairment concentrations are given. These values imply decreases in the total number of young produced as compared with the controls or the maximum production at a low metal concentration. Reproduction was usually stimulated by small metal additions. The 16% reproductive-impairment concentration is given since it represented a minimal reproducible value below which the variability in reproduction could not be detected from controls.

Chemical Measurements

Chemical characteristics of Lake Superior water (Table 1) were monitored during the testing period according to procedures outlined by the American Public Health Association et al. (1960) and procedures employing atomic absorption spectroscopy.

Table 2. Added and measured amounts (μg/liter) of some of the metal ions in test containers.

Metal ion	Added amounts	Measured amounts		No. samples
		Mean	Range	
Sodium	1,000,000	1,102,500	1,020,000–1,200,000	4
	1,500,000	1,550,000	1,380,000–1,770,000	4
Calcium	0	15,500	14,000–17,700	7
	31,200	48,000	–	1
	62,500	79,000	–	1
	100,000	120,000	113,100–116,000	3
	139,000	140,000	–	1
	200,000	227,200	210,800–258,600	6
	250,000	272,800	250,500–290,900	7
	300,000	315,600	294,900–341,400	4
	400,000	420,700	404,000–440,400	7
	500,000	513,100	492,900–533,300	5
Magnesium	100,000	101,300	96,000–106,000	8
	250,000	241,300	220,000–256,000	8
Potassium	60,000	54,800	47,000–61,000	8
	100,000	102,800	90,000–114,000	8
Iron	5000	4400	3400–5300	4
	10,000	10,100	9200–10,500	4
Manganese	5000	4800	4600–4900	8
	10,000	9400	9100–9900	8
Zinc	25	35	28–41	3
	50	52	43–61	4
	100	105	99–111	4
	125	125	100–150	4
	200	208	196–220	3
Cadmium	25	23	21–24	4
	50	43	40–47	4

American Chemical Society reagent-grade chemicals were used for all testing. They were: NaCl, $CaCl_2 \cdot 2H_2O$, $MgCl_2 \cdot 6H_2O$, KCl, $SrCl_2 \cdot 6H_2O$, $BaCl_2 \cdot 2H_2O$, $FeCl_3 \cdot 6H_2O$, $MnCl_2 \cdot 4H_2O$, $Na_2HAsO_4 \cdot 7H_2O$, $SnCl_2 \cdot 2H_2O$, $CrCl_3 \cdot 6H_2O$, $AlCl_3$, $ZnCl_2$, $HAuCl_4 \cdot 3H_2O$, $NiCl_2 \cdot 6H_2O$, $PbCl_2$, $CuCl_2$, $H_2PtCl_6 \cdot 6H_2O$, $CoCl_2 \cdot 6H_2O$, $HgCl_2$, and $CdCl_2 \cdot 2\frac{1}{2}H_2O$. Fresh stock solutions were prepared in lake water for each experiment except for Fe and Al, which were aged for at least 4 days to allow them to become chemically equilibrated before being used for testing animals.

Analytical measurements in test containers (Table 2) were made for Na, Ca, Mg, Fe, Mn, Zn, and Cd at the time of addition and 1 week later. In addition, stock solutions of Cu and Cd were monitored. All concentrations given in this paper are amounts added.

Dissolved oxygen concentrations in test containers were near saturation at all times. At dawn, before the lights came on, the concentration was ~9 mg/liter; late in the day oxygen sometimes slightly exceeded saturation because of photosynthesis by algae.

Hydrogen Ion Concentration

Measurements of *p*H were made in test containers when the medium was added and 1 week later when the medium and toxicant were replaced by fresh solutions. At or below concentrations having a chronic partial effect (i.e. on long term survival and reproduction), additions of As, Au, Ba, Ca, Cd, Co, K, Mn, Na, Ni, Sn, Sr, or Zn did not alter the *p*H by more than 0.3 of a unit above or below control water. However, at an Al concentration of 5000 μg/liter the *p*H rose from 6.5 to 7.5 after 1 week; at a Cr concentration of 5000 μg/liter it rose from 7.0 to 7.7; and at an Fe concentration of 10,000 μg/liter it rose from 6.4 to 7.6.

Biochemical Analyses

For weight measurements and biochemical analyses, all daphnids at a given concentration for a particular metal experiment were pooled. Three-week-old animals were collected on paper toweling, transferred to small plastic cups, dried (over $CaCl_2$) to a constant weight (minimum of 48 hr) at –20 C, and weighed. The average weight per animal was calculated. They were then transferred to 40-ml conical centrifuge tubes containing a small amount of powdered glass to which 200 μl of acetate buffer (0.05 M, *p*H 7.4) were added. A stainless steel stirring rod, ground to fit the contour of the tubes was rotated by motor at medium speed for 1 min to disintegrate the samples, which were then further homogenized by sonic cell disruption for 20 sec using a microprobe.[2] After centrifugation for 10 min at 1 C, the supernatant was withdrawn for protein and enzyme analysis.

With Technicon Auto-Analyzer modules and methodologies for total protein and SGOT[3], a manifold was assembled to analyze the two factors simultaneously. Samples were analyzed at the rate of 50/hr (sample:wash = 1:3) with control or reference samples spaced between every 10 unknowns. The protein system was operated on 2× scale expansion. The reference material for protein was an analytical control[4] and, for GOT,Versatol-E[5].

Results

Acute Tests

For all of the metals that were tested on an acute basis, median lethal concentrations were higher with than without food added (Table 3). Calcium and copper were more toxic in terms of 48-hr LC50 values without food than in terms of the 3-week 16% reproductive impairment values with food. Many of the metals tested were from one to two orders of magnitude more toxic on a chronic basis than in 48-hr tests.

Chronic Tests

In the 3-week studies reproductive impairment was found to be a more sensitive measure of toxicity than survival. For all the metals tested (Table 4)

Table 3. Acute (48-hr) and chronic (3-week) toxicities of various metal ions (μg/liter) to *Daphnia magna* in Lake Superior water.

Metal ion	Acute test: LC50		Chronic test: 16% reproductive impairment (with food)
	Without food	With food	
Sodium	1,640,000	1,820,000	680,000
Calcium	52,000	464,000	116,000
Magnesium	140,000	322,000	82,000
Potassium	93,000	166,000	53,000
Strontium	125,000	–	42,000
Barium	14,500	–	5800
Iron	–	9600	4380
Manganese	9800	–	4100
Arsenic	7400	–	520
Tin	–	55,000	350
Aluminum	3900	–	320
Zinc	100	280	70
Nickel	510	1120	30
Lead	–	450	30
Copper	9.8	60	22
Cobalt	1110	1620	10
Mercury	5	–	3.4
Cadmium	65	–	0.17

[2]Sonifer Cell Disruptor, Heat Systems Co., Melville, L.I., N.Y. 11749.

[3]Technicon Instrument Co., Tarrytown, N.Y. 10591. Methods: Total protein N86; SGOT (GOT) N25b.

[4]Pentex Biochemicals, Miles Laboratories, Kankakee, Illinois 60901.

[5]General Diagnostics Div., Warner–Lambert Pharmaceutical Co., Morris Plains, N.J. 07950.

TABLE 4. Chronic (3-week) toxicities of various metal ions (μg/liter) to *Daphnia magna* in Lake Superior water.

Metal ion	LC50	Reproductive impairment	
		50%	16%
Sodium	1,480,000 (1,180,000–1,840,000)[a]	1,020,000	680,000
	S 2.22[b]	S 1.50	
Calcium	330,000 (308,000–353,000)	220,000	116,000
	S 1.36	S 1.94	
Magnesium	190,000 (167,000–217,000)	125,000	82,000
	S 2.00	S 1.63	
Potassium	97,000 (87,000–108,000)	68,000	53,000
	S 1.42	S 1.28	
Strontium	86,000 (82,000–90,000)	60,000	42,000
	S 1.14	S 1.39	
Barium	13,500 (12,200–15,000)	8900	5800
	S 1.45	S 1.55	
Iron	5900 (5180–6730)	5200	4380
	S 2.15	S 1.18	
Manganese	5700 (5380–6040)	5200	4100
	S 1.24	S 1.29	
Arsenic	2850 (2520–3220)	1400	520
	S 1.63	S 2.66	
Tin	42,000 (23,000–76,000)	1500	350
	S 5.86	S 4.41	
Chromium	2000 (650–2600)	600	330
	S 3.70	S 1.82	
Aluminum	1400 (1080–1820)	680	320
	S 2.24	S 2.14	
Zinc	158 (146–170)	102	70
	S 1.40	S 1.48	
Gold	1050 (861–1281)	180	60
	S 1.65	S 3.00	
Nickel	130 (98–173)	95	30
	S 2.03	S 3.16	
Lead	300 (236–381)	100	30
	S 2.52	S 3.36	
Copper	44 (35–55)	35	22
	S 1.83	S 1.60	

(*Continued*)

TABLE 4. Chronic (3-week) toxicities of various metal ions (μg/liter) to *Daphnia magna* in Lake Superior water. — (*Concluded*)

Metal ion	LC50	Reproductive impairment	
		50%	16%
Platinum	520	82	14
	(437–619)		
	S 1.51	S 6.22	
Cobalt	21	12	10
	(14–31)		
	S 1.62	S 1.21	
Mercury	13[c]	6.7	3.4
	(9–19)		
	S 3.16	S 1.99	
Cadmium	5	0.7	0.17
	(4.0–6.2)		
	S 2.42	S 4.06	

[a]Ninety-five percent confidence limits.
[b]Slope function.
[c]Extrapolated value from three partial concentrations less than the LC50.

mean concentrations for 50% reproductive impairment were lower than 3-week LC50's. However, survival and reproduction were not significantly different for the following metals: Fe, Mn, Cr, Ni, Cu, and Co. The differences between survival (LC50) and reproductive impairment (50%) for the following elements, although significant, were less than twofold: Na, Ca, Mg, K, Sr, Ba, Al, Zn, and Hg.

TABLE 5. Effects of 3-week exposures to metal chlorides on body weight, total protein, and GOT acitivity of *Daphnia magna* (expressed as mean percentage deviation from control means).[a]

Metal ion	No. experiments	Effect concentrations		Weight/animal % Δ	Protein/animal % Δ	GOT/animal % Δ
		In M × 10^6	In μg/liter			
Sodium	3	43,500	1,000,000	−18	−7	+12
Calcium	2	10,000	400,000	−29	+18	+3
Magnesium	2	10,300	250,000	−22	+40	+65
Potassium	2	2040	79,800	+27	−5	+5
Strontium	2	1140	99,900	−24	+15	+55
Barium	1	144	19,800	−12	0	+1
Iron	1	134	7480	−77	+48	−13
Manganese	3	91.0	5000	−8	+24	+100
Arsenic	4	13.3	996	−18	−15	−18
Tin	2	25.3	3000	−23	+5	+15
Chromium	4	11.9	619	−11	−3	−4
Aluminum	2	23.0	620	−38	+3	−13
Zinc	1	2.68	175	−28	+10	+1
Nickel	2	2.13	125	−43	−9	−26
Lead	3	0.300	62	−12	+8	+15
Copper	3	0.628	40	−26	−5	−10
Platinum	2	0.318	62	−12	−13	−20
Cobalt	1	0.423	24	−15	+12	+45
Mercury	1	0.050	10	−5	−5	−19
Cadmium	1	0.0089	1	−7	+6	+15

[a]Precision (range) = ±10% (weight); 8% (protein); ±5% (GOT).

For the remaining elements: As, Sn, Cr, Au, Pb, Pt, and Cd; the difference was more than a twofold one; this was particularly striking with Sn, Au, Pb, and Cd.

Biochemical Measurements

Changes in body weight, total protein, and GOT activity induced by metal concentrations above 16% reproductive impairment levels were each computed by considering changes from the mean values of the controls run for each element. As many as 12 concentrations were tested for each metal although only one concentration is given in Table 5. The metal cations, with the exception of potassium, when added in concentrations having a measurable effect on survival or reproduction, caused a decrease in animal weight. The percentage of protein per animal was notably greater with Ca, Mg, Sr, Fe, Mn, Zn, and Co added, whereas it was less with As and Pt added. Changes when the other elements were added were slight. GOT activity was stimulated appreciably by Na, Mg, Sr, Mn, Sn, Pb, Co, and Cd additions; it was inhibited by Fe, As, Al, Ni, Cu, Pt, and Hg additions. The remaining elements caused only slight alterations in GOT activity.

Discussion

Comparative Toxicity

When 64-hr apparent thresholds (immobilization of 50% of the animals) for daphnids (Anderson 1950) are compared with 3-week LC50 values and 16% reproductive impairment levels, similarities in toxicity are evident for many metals, but large differences are apparent for others (Table 6). When 3-week LC50 values are compared with 64-hr apparent threshold concentrations, the results are similar for Na, Ca, Mg, Sr, Ba, Fe, Al, Zn, and Cd. Our chronic tests gave lower values for K, Mn, Ni, Pb, and Co; but higher values for Sn, Zn, Cu, and Hg. When our values for 1, 2, 4, 7, 14, and 21 days were plotted, we found that true threshold

Table 6. Chronic toxicities of metal ions to *Daphnia magna* in Lake Superior water and the 64-hr apparent thresholds in Lake Erie water.

	Lake Superior water:[a] chronic tests			Lake Erie water:[b] 64-hr apparent threshold	
	LC50	16% reproductive impairment			
Metal ion	μg/liter	μg/liter	Molarity × 10^{-3}	μg/liter	Molarity × 10^{-3}
Sodium	1,480,000	680,000	29.6	1,450,000	63.0
Calcium	330,000	116,000	2.89	332,000	8.3
Magnesium	190,000	82,000	3.40	189,000	7.8
Potassium	97,000	53,000	1.4	226,000	5.8
Strontium	36,000	42,000	0.48	<<63,000	0.72
Barium	13,500	5800	0.04	19,100	0.14
Iron	5900	4380	0.078	<6200	0.11
Manganese	5700	4100	0.075	21,800	0.40
Arsenic	2850	520	0.0069	–	–[c]
Tin	42,000	350	0.0029	16,000	0.13
Chromium	2000	330	0.0063	<<1200	0.023
Aluminum	1400	320	0.012	<1400	0.052
Zinc	158	70	0.0011	<<72	0.0011
Gold	1050	60	0.00030	–	–
Nickel	130	30	0.00051	<317	0.0054
Lead	300	30	0.00014	931	0.0045
Copper	44	22	0.00034	13	0.0002
Platinum	520	14	0.000072	–	–
Cobalt	21	10	0.00016	<1400	0.024
Mercury	13	3.4	0.000017	<4	0.000022
Cadmium	5	0.17	0.0000015	<<1.6	0.000014

[a] See Table 4.
[b] As adapted from Anderson (1950). His values were given in terms of the salts added; they are given here in terms of the metal ions.
[c] Anderson (1946) reported a 48-hr threshold value of $<0.11 \times 10^{-3}$.

values (as defined by Anderson 1950) for Na, Ca, Mg, K, and Fe were not obtained in 3 weeks. Our results suggested that true threshold values would probably be obtained only at or near 16% reproductive impairment concentrations. When comparisons are made between 64-hr apparent thresholds and 50% reproductive impairment (Tables 6 and 4), Zn and Cu were more toxic under the conditions tested by Anderson (1950), whereas all other metals were more toxic under our chronic test conditions.

Reproductive impairment levels (16%), when compared with apparent thresholds (Table 6), revealed that the only metal tested that Anderson (1950) found more toxic was Cu. Our chronic safe levels for Sn, Cr, Al, Ni, Pb, and Cd were considerably lower than 64-hr apparent thresholds. Differences between the chemistry of Lake Erie water and that of altered Lake Superior water, along with differences in the testing methods, particularly exposure times, probably account for the differences in toxicity. Anderson (1950) pointed out that "true thresholds" were lower than (<) or much lower than (<<) the concentrations given for Sr, Fe, Cr, Al, Zn, Ni, Co, Hg, and Cd; and suggested that tests of longer duration were needed. Our findings (Table 6) substantiate his remarks.

The organic material added as food altered the toxicity, as was evident in the 2-day experiments (Table 3). Thus, the results we obtained are not applicable directly as criteria for any particular water, but rather should be interpreted on a comparative basis as here reported. In more eutrophic waters daphnids may be tested in unaltered water.

For comparison, daphnid chronic toxicity values and those for other aquatic organisms reported by other investigators are presented in Table 7. The 16% reproductive impairment levels for Cr, Cu, and Zn to daphnids were similar to those for gammarids and fish, even though different compounds, water

TABLE 7. "Safe" concentrations of metal ions for aquatic animals tested through a complete generation under laboratory conditions.

Metal	"Safe" concentration (μg/liter)	Water hardness (as $CaCO_3$ in mg/liter)	Species
Chromium			
$CrCl_3$	330	45	*Daphnia magna*[a]
$Na_2Cr_2O_7$	200–400	45	*Salvelinus fontinalis*[b]
Copper			
$CuCl_2$	22	45	*Daphnia magna*[a]
$CuSO_4$	10.6	31.4	*Pimephales promelas*[c]
$CuSO_4$	14.5	198	*Pimephales promelas*[d]
$CuSO_4$	4.6–8.0	45	*Gammarus pseudolimnaeus*[e]
$CuSO_4$	9.5	45	*Salvelinus fontinalis*[f]
Zinc			
$ZnCl_2$	70	45	*Daphnia magna*[a]
$ZnSO_4$	<180	203	*Pimephales promelas*[g]
Cadmium			
$CdCl_2$	0.17	45	*Daphnia magna*[a]
$CdSO_4$	37	200	*Pimephales promelas*[h]
Nickel			
$NiCl_2$	30	45	*Daphnia magna*[a]
$NiSO_4$	400	200	*Pimephales promelas*[i]

[a]From Table 4, 16% reproductive impairment concentrations.
[b]D. A. Benoit (personal communication), National Water Quality Laboratory, Duluth, Minn.
[c]Mount and Stephan (1969).
[d]Mount (1968).
[e]Arthur and Leonard (1970).
[f]McKim and Benoit (1971).
[g]Brungs (1969).
[h]Pickering and Gast (1972).
[i]Pickering (1972).

hardnesses, and associated water quality were tested. Nickel and cadmium were much more toxic to *D. magna* in soft water than to fathead minnows in hard water.

Biochemical Measurements

After 3 weeks, daphnids exposed to metals weighed less than control animals. In addition, the test animals appeared to be smaller, but they may have been carrying fewer young. The reasons for increases in protein and GOT activity are not clear; possibly the molecular dynamics of the animals, such as those involving induction effects on protein-forming enzymes, were changed, thus causing a general increase in protein metabolism.

Toxicity and Physicochemical Correlations

The metal-ligand forms present in the water at the time of uptake by the organisms and their specific toxicities are unknown. Certain correlations were found between the toxicity of these metals and their physicochemical characteristics. When the –log molarity (as *p*M) at the 16% reproductive impairment level was compared with the –log K_{sp} (as pK_{sp}) of the metal sulfides, a correlation coefficient of 0.6 ($P < 0.05$) (Fig. 1) was found. The correlation between toxicity and the solubility of metal sulfides suggests the possibility that the metals may combine in vivo with sulfhydryl groups on enzymes, which affects their solubility and catalytic activity.

Another correlation, involving more of the elements, was obtained for the *p*M against the electronegativity. This correlation coefficient was 0.78 ($P < 0.01$) and agrees with a similar plot by Somers (1969) using *Botrytis fabae* as the test organism. In a similar manner the toxicity of 11 elements was correlated with the log K_{eq} of the metal–ATP complex (Martell 1964). The correlation coefficient was 0.74 ($P < 0.01$).

Physicochemical constants of the metal elements that were analyzed but showed no definite correlation with toxicity included standard electrode potential, covalent radius, atomic radius, ionic radius, first ionization energy, electrical conductivity, atomic weight, atomic number, density, and equilibrium constants of certain of the metal ions with cysteine, aspartic acid, histidine, histamine, arginine, imidazole, glycylglycine, glutathione, and carboxpeptidase A.

To clarify the mechanisms of toxic action of pollutants on aquatic organisms, further concurrent studies on whole animals and on specific molecular processes should be encouraged. This double approach makes possible direct correlations between

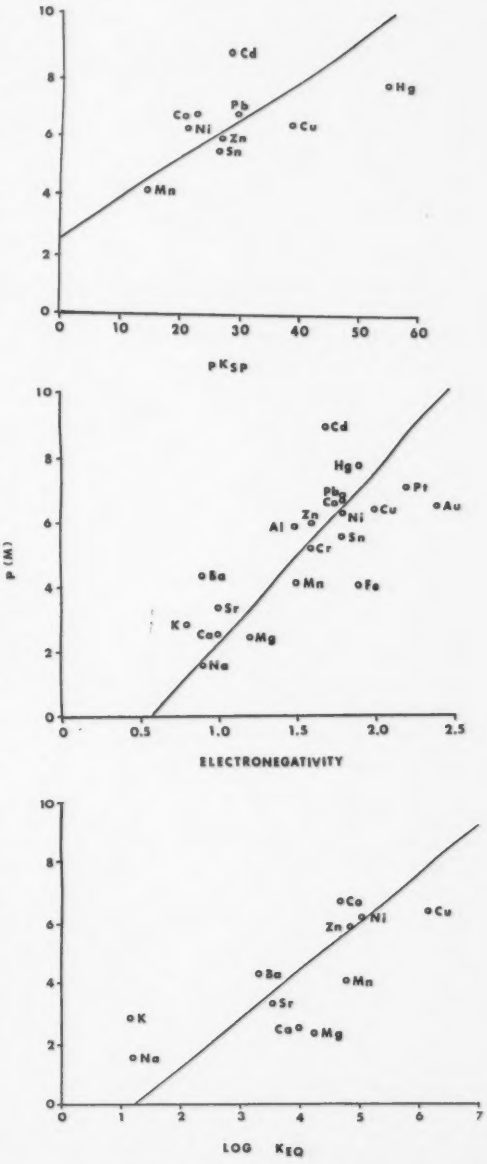

FIG. 1. Correlations between the 16% reproductive impairment concentration for *Daphnia magna* of metals as *p*M (–log molarity) and their solubility product constants as metal sulfides (pK_{sp}), their electronegativity (according to Pauling 1960), and their equilibrium constants as the metal-adenosine triphosphate complex (log K_{eq}). (Lines were fitted using the method of least squares.)

specific chemical events and effects upon the complete animal. Thus, key processes and significant interactions regarding in the mec hanism of toxicity may be revealed. Although we have considered only simple metal and ion forms, it is not implied that they are the only ones present. If the exact molecular compositions and conformations of all reagents, including the test water, were known, perhaps there would be a much closer agreement between chemical properties and toxicity.

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Growth, Life History, and Respiration of *Mysis relicta* in an Arctic and Temperate Lake[1,2]

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LASENBY, D. C., AND R. R. LANGFORD. 1972. Growth, life history, and respiration of *Mysis relicta* in an arctic and temperate lake. J. Fish. Res. Bd. Canada 29: 1701–1708.

Mysis relicta from Char Lake (N.W.T.) take 2 years to reach maturity, retaining 36 cal as net production; those from Stony Lake (southern Ontario) mature in 1 year, retaining 53 cal as net production. Growth rates were highest during summer months for individuals in both lakes. Results of respiration experiments at 0, 2, 4, 6, and 8 C for Char Lake mysids and at 2, 4, 7, 10, and 13 C for Stony Lake mysids were not significantly different, indicating that *Mysis relicta* demonstrates no metabolic compensation over its environmental temperature range. Generalized energy budgets were constructed for individuals from each population for their entire life-span. A female uses approximately 209 cal for growth and respiration to become a reproducing adult in one year in Stony Lake and approximately 206 cal to become a reproducing adult in 2 years in Char Lake.

LASENBY, D. C., AND R. R. LANGFORD. 1972. Growth, life history, and respiration of *Mysis relicta* in an arctic and temperate lake. J. Fish. Res. Bd. Canada 29: 1701–1708.

Mysis relicta du lac Char (Territoires du Nord-Ouest) atteint la maturité en 2 ans, maintenant une production nette de 36 cal. Celle du lac Stony, dans l'Ontario méridional, atteint la maturité en 1 an, maintenant une production nette de 53 cal. Le taux de croissance pour les échantillons des deux lacs est le plus élevé pendant les mois d'été. Les résultats d'expériences sur la respiration effectuées à 0, 2, 4, 6, et 8 C pour les mysides du lac Char, et à 2, 4, 7, 10 et 13 C pour ceux du lac Stony ne révèlent pas de différences significatives. Il n'y a donc pas, chez *Mysis relicta*, de compensation métabolique en relation avec les variations de température de l'environnement. Les auteurs élaborent des budgets énergétiques généralisés chez les individus de chaque population pour leur vie entière. Une femelle du lac Stony utilise environ 209 cal pour la croissance et la respiration et devient adulte reproductrice en un an, et une femelle du lac Char consume environ 206 cal pour la croissance et la respiration et devient adulte reproductrice en 2 ans.

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SEVERAL hypotheses have been suggested to explain the phenomenon that many invertebrates in the arctic exhibit a 2-year life cycle, as opposed to a 1-year life cycle in temperate zones (Dunbar 1968; McLaren 1966). Also, some results have been recorded for marine animals that are consistent with the hypothesis that poikilotherms may extend their range of distribution by metabolic compensation for changes in environmental temperatures (Scholander et al. 1953; Bullock 1955). The present study was undertaken to determine whether or not the life cycles and metabolic rates of representative individuals from two populations of the glacial relict crustacean *Mysis relicta* Lovén were consistent with the above observations. To compare life histories, the number of calories retained for growth and reproduction was determined throughout the lifespan of individuals from Char Lake, N.W.T. (74°42′N, 94°54′W), and from Stony Lake in southern Ontario (78°05′ W, 44°35′N). To determine if metabolic compensation occurred within the species (i.e. if respiration rates of *M. relicta* at each environmental temperature were similar), the respiration rates at different temperatures over the environmental temperature range of mysids from each lake were compared. In addition, the number of calories a representative mysid

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from each lake expended in respiration throughout its life-span was estimated. This allows a comparison of the growth and respiration of representative animals of the two populations as well as a comparison of the total energy utilized throughout the life-span of the animals.

Growth and Life History

Figure 1 gives the distribution frequency of different size classes of *Mysis* in the two lakes. Length was measured under a dissecting microscope at a magnification of 40×.

The Char Lake population of *Mysis* on February 16, 1970, had a trimodal structure, comprised of three cohorts: 8–9-month-old immature mysids, 20-month-old adult male and female mysids, and 32-month-old adult female mysids (Fig. 1B). Figure 2A shows the results of plotting the mean size of immatures, males and females of each cohort from monthly catches, against time. Young mysids are released from the brood pouch when they are 3.5–4.0 mm long. After approximately 12 months they begin to separate into two size classes and, by September, when they are approximately 18 months old, the smaller animals have become mature males and the larger animals mature females. At this time the females begin to carry eggs in the brood pouch and these develop over winter. After nine months the young mysids are released. Most males die a few months after mating (i.e. February of their second year).

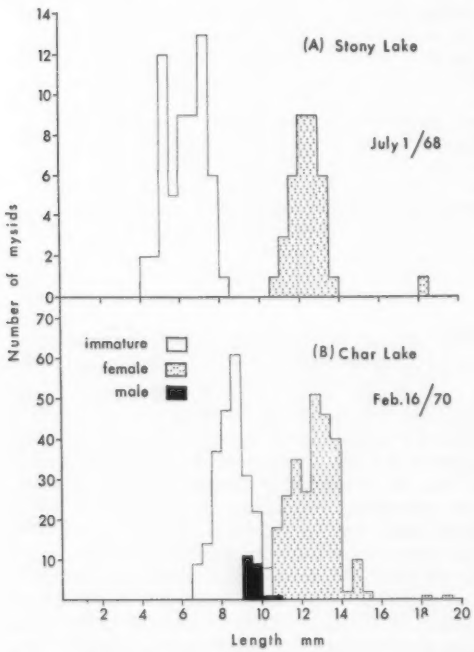

FIG. 1. Length distribution of mysids in population samples from (A) Stony Lake, and (B) Char Lake. Three distinct cohorts in each population are shown.

To obtain growth in dry weight, animals were measured and dried at 60 C to a constant weight (Lovegrove 1966) and the following length–weight relation determined:

$$Y = 0.00272\ X^{2.00} \quad (1)$$

where Y is the dry weight in milligrams and X is the length in millimeters. The average monthly increase in length was determined from Fig. 2A and changed to an increase in dry weight by equation (1).

To express dry weight in calories a value of 5.4 ± 0.4 S.D. cal/mg dry weight was obtained by bomb calorimetry of mysids from Char Lake using the Gentry–Weigert modification of Phillipson's (1964) microbomb calorimeter. The increase in dry weight was multiplied by this caloric value, results therefore being expressed as cal/animal/month (see Fig. 3A).

Each Char Lake female carries 12 eggs (range 5–22, n = 75) and the dry weight of each egg is approximately 0.12 mg. A caloric value of 5.4 cal/mg was used to convert this dry weight to calories (assumed to be same as adult mysid, although this may actually be somewhat low). Therefore, each Char Lake female mysid retains approximately 7.8 cal for egg production over a period of 2 years.

In Stony Lake the population in July 1968 was also trimodal, consisting of 2-month-old immatures, 1-year-old adult females, and a few 2-year-old female mysids. The mean length of each cohort for the monthly catches was plotted against time to give the growth of the mysids (Fig. 2B).

The females lay eggs in the brood pouch in December. The embryos take 5 months to develop in the brood chamber. Immature mysids about 4 mm long were released from the brood pouch of the females in May and became recognizable as males and females 5 months later in September. The males die off 2–3 months after mating.

For growth in weight, the following length–weight relation was determined as for Char Lake animals:

$$Y = 0.00345\ X^{2.84} \quad (2)$$

where Y is the dry weight of the mysid in milligrams and X is the length of the mysid in millimeters. The average monthly increase in length was determined from Fig. 2B and changed to an increase in dry weight by equation (2).

A value of 5.9 ± 0.2 S.D. cal/mg dry weight was obtained by bomb calorimetry. This value multiplied by the monthly increase in dry weight gave the mysid growth rate in cal/animal/month (see Fig. 3B).

Each Stony Lake female carries 12 eggs (range 10–14, n = 22). Each egg weighs 0.20 mg. Therefore, each female retains approximately 2.4-mg dry weight for the production of egg material. Using a caloric value of 5.9 cal/mg dry weight for the eggs, the female retains ap-

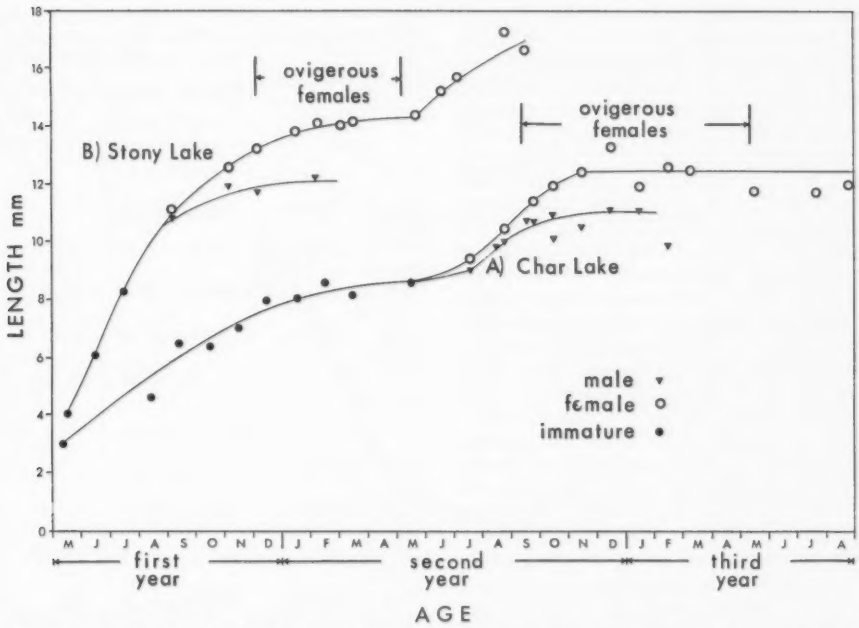

FIG. 2. Average length of each cohort for samples taken at approximately monthly intervals from Char and Stony lakes. Data are presented to illustrate increase of mysid length throughout its life-span. Ovigerous females are indicated.

proximately 14 cal in egg production as compared with 7.8 cal for Char Lake females.

Respiration

Mysids were collected from the lakes and acclimated to the experimental temperatures 24 hr before respiration measurements were made. The mysids to be tested at each temperature were divided into two separate size-groups, immature and adult. Both before and between measurements mysids were supplied with ample food.

Respiration experiments to determine the oxygen consumption of both immature and mature mysids were carried out at 2, 4, 7, 10, and 13 C for Stony Lake mysids and 0, 2, 4, 6, and 8 C for Char Lake mysids.

For the measurement of oxygen consumption the mysids were transferred into glass-stoppered bottles, which had previously been filled with air-saturated water at the required temperature, and immediately placed in the experimental bath. Similar sized individuals were chosen for each bottle. Although there are several criticisms of the closed bottle technique (Kamler 1969), it was considered to be the best method for measurement of the oxygen consumption of *M. relicta* because it disturbs the mysid very little and the animal has a relatively large volume in which to swim. The following numbers of animals and bottle sizes were used for the experiments: Char Lake adults and young, 5 and 10 mysids, respectively, in 150-ml bottles; Stony Lake adults and immatures, 4 in 250-ml bottles and 10 in 150-ml bottles, respectively. Controls with no mysids in the bottles were run with each experiment. The mysids remained in the sealed bottles for approximately 5 hr, except that the immatures at 0 and 2 C were held for 8 hr. At the end of each run, the water was siphoned from the experimental and control bottles into 60-ml ground-glass stoppered bottles. The oxygen content of these subsamples was determined using the azide modification of the Winkler method (American Public Health Association et al. 1965). The Winkler titrations were made with 0.05-N sodium thiosulfate, using a "Gilmont" micrometer burette of 2.5-ml capacity. The difference in oxygen content of the water from experimental and control bottles was considered to be the result of the oxygen uptake by the mysids.

The relation between body weight and oxygen consumption may be represented by the equation:

$$O_2 = aW^k \text{ or } \ln O_2 = \ln a + k \ln W \qquad (3)$$

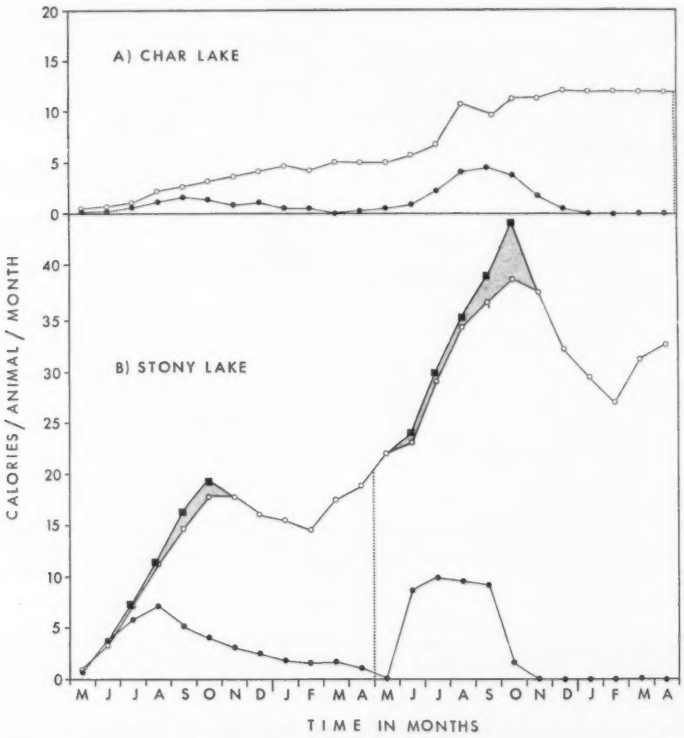

FIG. 3. Growth and respiration rates in calories/animal/month for (A) Char Lake mysids and (B) Stony Lake mysids for each month throughout their life-span. Solid squares represent the number of calories expended in respiration as a result of the temperature changes encountered during vertical migration in Stony Lake. Broken line indicates generation time.

in which O_2 is the oxygen consumption in milligrams/animal/hour, W is the body weight in milligrams, a (the oxygen consumption of a 1-mg mysid at a particular temperature) is the intercept, and k is the slope of the *ln–ln* plot of oxygen consumption/animal/hour versus weight of animal (Weymouth et al. 1944). The values of a and k of the regression equations fitted for both Char and Stony Lake data at each temperature are given in Table 1. Analysis of covariance showed that none of the values of k differed significantly from the mean value of 0.75. Hence, the value 0.75 was used as a weight correction in all subsequent calculations. The value of 0.75 is a common value found for the relation between metabolic rate and size (Zeuthen 1953). Analysis of covariance also demonstrated that the a values at different temperatures in Table 1A as well as in Table 1B were significantly different from one another. Analysis of covariance also indicated that there was no significant difference between the Char and Stony Lake respiration rates over the temperature range of 2–8 C.

Char Lake mysids consume almost 50% less oxygen than those of Stony Lake at their mean annual environmental temperatures of 0.9 and 5.3 C (0.00143-mg O_2/mg dry wt/hr and 0.00203-mg O_2/mg dry wt/hr, respectively, see Table 1). Since there was no statistically significant difference between the Char Lake and Stony Lake respiration rates over the temperature range of 2–8 C, metabolic compensation does not appear to occur with *Mysis relicta*. If mysids did compensate for temperature, one would expect that activity at their respective environmental temperatures would be similar. Char Lake mysids appear to be much more lethargic than Stony Lake mysids at their respective environmental temperatures.

TABLE 1. Relation between mysid oxygen consumption (Y) and dry weight of mysid (W) at different temperatures in Char and Stony lakes; $Y = aW.^{k}$

Temp (C)	n	$k \pm 95\%$ CI	$a \pm 95\%$ CI
		(A) Char Lake	
0	8	0.776±0.085	0.00136+0.00014 −0.00012
2	10	0.734±0.052	0.00152+0.00007 −0.00006
4	10	0.723±0.080	0.00202+0.00013 −0.00013
6	6	0.779±0.140	0.00241+0.00030 −0.00027
8	6	0.747±0.114	0.00265+0.00035 −0.00031
		(B) Stony Lake	
2	6	0.819±0.075	0.00151+0.00018 −0.00015
4	17	0.739±0.056	0.00182+0.00017 −0.00014
7	18	0.702±0.044	0.00230+0.00014 −0.00014
10	18	0.736±0.050	0.00265+0.00020 −0.00020
13	18	0.764±0.036	0.00307+0.00017 −0.00017

These results of the respiration experiments do not agree with the statement made by Bullock (1955) that "adaptation of metabolism and other rate functions to latitude, as though it were compensation for temperature, is widespread, within and between species." Many of the observations considered by Bullock were not made on animals of the same species and, when made within species, they were not made on animals of the same size. This may account for the differences in our conclusions.

To determine if there were any major differences in the respiratory requirements for the entire life-span of the mysids from the two lakes, it was necessary to estimate the amount of energy a representative mysid from each lake expends in respiration throughout its life. To do this it is necessary to relate the laboratory oxygen consumption rates to in situ oxygen consumption rates. When doing this, it must be realized that these can be only rough estimates, since the assumption is made that the animal behaves under laboratory conditions the same as it behaves in nature.

When determining the oxygen consumption of an animal throughout its life-span, the sizes of the animal and the temperatures at which it lives must be considered. Since Char Lake mysids do not migrate vertically, mean monthly temperatures encountered by the animals at 10 m were determined (Table 2). This depth was chosen as this is where the greatest density of mysids was found. The lengths used were taken as the average for each month and this was converted to dry weight by equation (1). Oxygen consumption in milligrams O_2/gram dry weight/hour for a 1-mg dry weight mysid at each mean monthly temperature was calculated from Table 1 and calculated for the mean monthly dry weight by equation (3) where $k = 0.75$. This value was then multiplied by an oxycaloric equivalent of 3.38 to express the oxygen consumption in calories (Teal 1957). By summing the number of calories spent on respiration during each month, it was found that a Char Lake female expends approximately 140 cal in respiration throughout its 21 month life-span.

Since Stony Lake mysids migrate vertically during summer, the effect of the change in temperature, related to migration, on rate of oxygen consumption was considered. Vertical migration was determined by means of vertical stage hauls at 5-m intervals with a #10 plankton net.

The mean depth of the population throughout the night was estimated. Mean depth of the mysid population at one particular time was determined by multiplying the number of mysids in a 5-m interval (see Table 3) by the depth of that interval,

TABLE 2. Mean monthly temperatures of lake water at particular depths in Char and Stony lakes and average temperature experienced by migrating immature and mature mysids in Stony Lake.

Date (1969)	Char Lake Temp (C) (10 m)	Stony Lake Temp (C)		
		Nonmigrator (27 m)	Migrator	
			immature	adult
May	0.40	5.45	–	–
June	0.80	6.30	9.08	8.27
July	2.00	6.80	9.55	8.49
Aug.	3.80	7.00	9.97	8.96
Sept.	1.00	7.35	10.00	9.63
Oct.	0.30	7.60	9.97	9.65
Nov.	0.30	6.50	–	–
Dec.	0.20	3.75	–	–
Jan.	0.20	2.32	–	–
Feb.	0.20	2.20	–	–
Mar.	0.20	3.20	–	–
Apr.	0.20	4.40	–	–
Avg annual temp	0.80	5.26		

summing the values, and dividing by the number of mysids, i.e. mean depth equals

The average for the night of July 1, 1968, was then determined and was found to be 14.2 m for the immature mysids and 17.4 m for the adult mysids. It was assumed that these "average mean depths" remained the same throughout the summer and fall period (June–November). This is not strictly valid as Brownell (MS 1970) found that, from early summer to late fall, there is a progressively earlier ascent and later descent. However, this would make little difference to the final results. The mean monthly temperatures encountered by a migrating mysid are given in Table 2. The fact that the mysid spends

TABLE 3. Vertical distribution of Stony Lake immature and adult mysids at night (July 1, 1968) together with mean depths of the population at intervals throughout the night. Omitting 2100 hr and 0500 hr, the average mean depths are 14.2 m for immature mysids and 17.4 m for adults.

Depth (*m*)	Time						
	2100	2300	0100	0200	0300	0400	0500
			Immature				
0–5	0	8	5	6	6	1	0
5–10	0	8	23	20	20	47	0
10–15	0	17	17	8	8	74	0
15–20	0	0	34	31	31	0	2
20–25	20	1	0	0	0	31	9
25–27	25	6	29	13	13	0	12
Mean depth	25.3	12.0	16.6	14.8	14.8	12.9	24.7
			Adult				
0–5	0	0	1	1	1	0	0
5–10	0	5	5	5	3	7	0
10–15	0	1	5	19	7	38	0
15–20	0	13	10	52	22	5	0
20–25	1	0	14	0	27	0	1
25–27	0	11	0	0	11	13	3
Mean depth	27	19.3	16.9	15.4	19.8	15.4	26.3

TABLE 4. Energy budgets in calories per individual female mysid from Char and Stony lakes, based on an assimilation efficiency of 85%. Ingestion is calculated by the simplified energetics equation, ingestion = growth + respiration + egestion; (.85I = G + R).

	Ingestion	=	growth	+	reproduction	+	respiration	+	egestion
				First year					
Char Lake	62	=	10	+	0	+	43	+	9
Stony Lake	245	=	39	+	14	+	156	+	36
				Second year					
Char Lake	180	=	18	+	8	+	127	+	27
Stony Lake	510	=	39	+	14	+	376	+	81
				Total					
Char Lake	242	=	28	+	8	+	170	+	36
Stony Lake	755	=	78	+	28	+	532	+	117

the daylight hours at 27 m was taken into consideration in these calculations, as well as the fact that the mysids are in shallow (15–20 m) inshore water during the day for the months of September and October.

$$\frac{\text{(no. mysids in interval} \times \text{mean depth of interval)}}{\text{total no. mysids}}$$

A migrating female mysid in Stony Lake expends approximately 547 cal in respiration, not considering the energy required for moving upward. A nonmigrating female mysid expends a total of 532 cal in respiration, or about 3% less than a migrating mysid for a life-span of 2 years. This, combined with the suggestion that the actual work involved in vertical migration is insignificant (Vlyman 1970), indicates that the respiratory cost of vertical migration constitutes a very small proportion of the total respiration of the animal. Figure 3B shows the difference in respiration rates in calories/animal/month between the migrating and nonmigrating mysids during the period June–October inclusive.

Energy Budgets

Table 4 is a summary of the average energy budgets of individual mysids from Stony and Char Lakes, assuming an assimilation efficiency of 85% (Lasenby MS 1971). Over a 2-year period (i.e. from hatching to maturity), the number of calories put into growth and reproduction of a Char Lake mysid (28 + 8) is approximately 68% of the number put into growth and reproduction of a Stony Lake mysid from hatching to maturity over a 1-year period (39 + 14).

Discussion

It is interesting to compare these results with the following statement made by Vernberg and Vernberg (1970): "If a more northern species moves to warm waters, the increased energy demands resulting from higher metabolic rates cause the animal literally to starve to death, and thereby limit its southern distribution". This statement fails to consider the fact that, in general, in fresh waters there is an increase in food available to the animal as it moves from cold oligotrophic northern waters to more southern waters. In general, temperate lakes have a higher production than arctic lakes. Dunbar (1968) infers this by stating that low production in lakes in the higher latitudes may be a result of low energy input to the system or low nutrients or a combination of these factors. *Mysis relicta* seems to have overcome the problems of life in warmer waters by developing behavioral mechanisms such as vertical migration to take advantage of the rich food supply in the epilimnion of temperate lakes while living in the cooler hypolimnion most of the time.

In the higher latitudes, *Mysis relicta* requires 2 years to reach maturity as opposed to 1 year in temperate zones. The 2-year life cycle for invertebrates in the Arctic is well documented in the literature (Dunbar 1968). What is also of interest is that Stony Lake female mysids use approximately 209 calories for growth and respiration to become reproducing adults in 1 year and Char Lake mysids use 206 cal to become reproducing adults in 2 years. The possibility that a species uses the same amount of energy to become a mature, reproducing adult regardless of its geographic location or the time to reach maturity is interesting to contemplate and should perhaps be further investigated.

Acknowledgments

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Morphological Differences in Male Gonads Among Nine Genera of Gadidae (Pisces)

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VLADYKOV, V. D. 1972. Morphological differences in male gonads among nine genera of Gadidae (Pisces). J. Fish. Res. Bd. Canada 29: 1709–1716.

Among 12 species of Gadidae, which belong to nine genera and three subfamilies, six basic types of male gonads are observed. In the freshwater genus, *Lota*, gonads are simple, nearly cylindrical in shape, and not subdivided into lobes. In the marine genera of cold waters, such as *Melanogrammus* and *Gadus*, the other extreme in gonad structure, consisting of numerous, rather uniform convolutions, is found. In the marine genera *Urophycis* and *Merluccius* of more temperate waters, the male gonads consist of several lobes, rather irregular in shape and size. Among genera inhabiting brackish and sometimes fresh water, such as *Microgadus*, *Boreogadus*, and *Eleginus*, the gonads are subdivided into lobes which are not very numerous. In the genus *Arctogadus*, distributed in salt and brackish Arctic waters, the gonads are intermediate in their complexity between the typical marine genera of cold water, *Melanogrammus* and *Gadus*, and those three genera inhabiting brackish waters. The explanation for the morphological differences in male gonads of Gadidae appears to be associated principally with the respective type of waters (salt or fresh) which they inhabit and their spawning requirements, and to a much lesser degree with their systematic relationships.

VLADYKOV, V. D. 1972. Morphological differences in male gonads among nine genera of Gadidae (Pisces). J. Fish. Res. Bd. Canada 29: 1709–1716.

Nous avons identifié six types fondamentaux de gonades mâles chez 12 espèces de Gadidae appartenant à neuf genres et trois sous-familles. Chez le genre d'eau douce, *Lota*, les gonades sont simples, de forme presque cylindrique, et ne sont pas subdivisées en lobes. La structure des gonades des genres marins des régions froides, tels *Melanogrammus* et *Gadus*, est à l'autre extrême: elles sont constituées de circonvolutions nombreuses et plutôt uniformes. Chez les genres marins *Urophycis* et *Merluccius* des eaux plus tempérées, les gonades mâles sont formées de plusieurs lobes, de forme et de grandeur plutôt irrégulières. Parmi les genres fréquentant les eaux saumâtres et parfois les eaux douces, comme *Microgadus*, *Boreogadus* et *Eleginus*, les gonades sont divisées en lobes peu nombreux. Les gonades d'*Arctogadus*, qui est réparti dans les eaux salées et saumâtres de l'Arctique, ont un degré de complexité intermédiaire entre les genres marins typiques des eaux froides, *Melanogrammus* et *Gadus*, et les trois genres habitant les eaux saumâtres. Ces différences morphologiques dans les gonades des Gadidae semblent être liées surtout au type d'eau (salée ou douce) dans laquelle ils vivent, à leurs exigences reproductrices et, à un degré beaucoup moindre, à leurs affinités systématiques.

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PUBLICATIONS dealing with Gadidae, an economically important group of fishes, are extremely numerous. Despite this, there appears to be an almost complete absence of information on the morphology of their gonads, especially of the male sex.

Publications by Scheuring (1941) and Vallin (1964) contain drawings and a short description of immature male gonads of the European burbot (*Lota lota*). Battle (MS 1951) presented semischematic drawings of male gonads of white hake (*Urophycis tenuis*). Homans and Vladykov (1954) discussed the stages of maturity for both female and male haddock (*Melanogrammus aeglefinus*) without illustrations of the gonads, but mentioned that the testes were "wavy". Powles (1958), in defining the sexual stages of Atlantic cod (*Gadus morhua*), described their testes as "wavy lobules".

Apparently, no comparative morphological study of male gonads of different gadid species or genera has been published. The present article may attract attention for further studies on this neglected subject.

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Materials and Methods

The gonads of 49 males and 1 female for this study were preserved in 4–5% formalin, from a few months to several years. The gonads of the Atlantic cod were kept in formalin for 37 years and their shape and general structure do not differ from recently obtained specimens.

To prevent distortion of the gonads, they were photographed submerged in water, and are shown from the dorsal surface with the posterior end located close to the tag. Their size can be ascertained by comparison with the plastic tags, which are 29 mm long and 8 mm wide. In some species, the mature or maturing gonads extend somewhat posteriorly beyond the anal opening.

Throughout the text and in Table 1, length of fish refers to fork length, but in Table 2 it refers to the total length.

Specimens bearing the label NMC were borrowed from the National Museum of Canada, Ottawa.

This study was made principally on mature gonads; the collecting details are given in Table 1. For each species, at least two individuals were examined, but for toothed cod (*Arctogadus borisovi*) only one specimen was available. Altogether, male gonads of 12 species of Gadidae, belonging to nine genera and three subfamilies, were studied. For the systematic definition of different subfamilies, the classification of Gadidae by Svetovidov (1948) was followed. A brief description of the gonads is given in Table 2, and their appearance is illustrated by the figures.

Subfamily Lotinae

Lota lota — In addition to the female and male referred to in Table 1, the following specimens in the prespawning condition (maturity stage 4–5) were studied: 2 males, 484 and 540 mm long, collected in Lake Simcoe, Ont., on November 4, 1970, by E. Skobe; 3 males, 445–695 mm long, obtained in Lake Temiscouata, Que., on January 15, 1971, by C. Veilleux. Gonads of the five males were of the same shape and appearance as that of the typical specimen, W 4735, in Fig. 1.

According to Pivnička (1970), our specimens of burbot from Eastern Canada belong to the subspecies *Lota lota lacustris* (Walbaum) 1792 (= *L. lota maculosa* (LeSueur) 1817). Observations on spawning of burbot in Lake Simcoe, Ont., were published by McCrimmon (1959).

Urophycis chuss — In addition to the typical specimen, W 4778, in Fig. 2, a male 507 mm long, with less advanced gonads (maturity stage 3), was available (NMC 62–82). It was collected west of Sable Island, N.S., on May 1, 1961, by S. W. Gorham. The morphology of the gonads in both specimens was quite similar in spite of the difference in the stages of maturity.

Subfamily Merlucciinae

Merluccius bilinearis — In addition to the typical specimen, W 4784, in Fig. 2, a male 318 mm long, with less developed gonads (maturity stage 3–4), was available (NMC 62–103). It was collected southwest of Sable Island, N.S., on May 7, 1961, by S. W. Gorham. In spite of the difference in stages of maturity, gonads of both were of the same type.

Subfamily Gadinae

Microgadus tomcod — In addition to the typical specimen, W 4752, in Fig. 3, which was in spawning condition, 8 males in the same stage of maturity were available. These specimens (175–179 mm) were collected in the St. Lawrence River near the Montmorency Falls, Que., on November 28, 1970, by G. Labrecque. Gonads of all specimens were of the same morphological type.

Microgadus proximus — In addition to the typical specimen, W 4749, in Fig. 3, which was in spawning condition, two males (180 and 260 mm) with gonads in the corresponding stage of maturity were available (NMC 59–147). They were collected at Point Grey, Vancouver, B. C., on December 14, 1955, by M. A. Newman. Gonads of these three specimens were of the same type.

Eleginus navaga — In addition to the typical specimen, W 4747, in Fig. 4, which was near spawning condition, 8 males (195–218 mm) in similar stages of maturity were available. They, and the type, were collected in the White Sea and kindly sent to me by Dr A. N. Svetovidov. These specimens were received in Ottawa on February 24, 1959, and apparently had been collected 1 or 2 years previously. The dorsal surface of gonads of the type (W 4747) and the other specimens was disfigured by imprints of the vertebral parapophyses, which are particularly well developed in this species. All male gonads have the same shape as the type.

Boreogadus saida — In addition to the typical specimen, W 4737, in Fig. 4, which was nearly in spawning condition, a specimen 215 mm long in the same stage of maturity was available. It was collected on October 22, 1944, in the St. Lawrence River at the estuary of the Rivière-Ouelle, Que., by V. D. Vladykov. The gonads of both specimens were of the same type.

Arctogadus glacialis — In addition to the typical specimen, W 4741, in Fig. 5, which was in prespawning condition (maturity stage 3–4), a specimen 345 mm long was available. This specimen, in about the same stage of maturity as the type, was collected in Hole-in-Fog Bay near Isachsen, N.W.T., on July 24, 1954, by S. D. MacDonald. The gonads of both specimens were of the same type.

Arctogadus borisovi — Only the typical specimen, W 4764, in Fig. 5, was available for this study. It was nearly in spawning condition. The morphology of its gonads, although distinct from that of *A. glacialis*, could be considered as belonging to the same type characteristic of the genus *Arctogadus*.

The identification of two species of *Arctogadus* was based on data by Nielsen and Jensen (1967) and Boulva (1972).

TABLE 1. Collecting data, lengths of fish, and details of gonads of 12 species of Gadidae illustrated here (all males except W 4734).

Tag No.	Species	For length of fish (*mm*)	Observations on gonads			Collecting data		
			Stage of maturity	Length[a] (*mm*)	Weight (*g*)	Date	Locality	Collector
W 4734	*L. lota* (female)	740	4	135	169.0	Nov. 4/70	Lake Simcoe, Ont.	E. Skobe
W 4735	*L. lota*	560	4–5	145	153.0	Nov. 4/70	Lake Simcoe, Ont.	E. Skobe
W 4778	*U. chuss*	368	4	70	10.7	May 1/61	Off Sable Is., N.S.	S. W. Gorham
W 4784	*M. bilinearis*	320	4	67	9.0	May 7/61	Off Sable Is., N.S.	S. W. Gorham
W 4752	*M. tomcod*	180	4–5	42	4.0	Nov. 28/70	St. Lawrence River near Montmorency Falls, Que.	G. Labrecque
W 4749	*M. proximus*	233	4–5	52	12.0	Dec. 14/55	Point Grey, Vancouver, B.C.	M. A. Newman
W 4747	*E. navaga*	200	4	48	5.0	Feb. 24/59[b]	White Sea	A. N. Svetovidov
W 4737	*B. saida*	165	4	54	4.5	Oct. 1/43	St. Lawrence River at Rivière-Ouelle, Que.	V. D. Vladykov
W 4741	*A. glacialis*	280	3–4	70	8.0	July 24/54	Hole-in-Fog Bay, N.W.T.	S. D. MacDonald
W 4764	*A. borisovi*	410	4–5	110	33.0	Sept. 4/68	Cambridge Bay, N.W.T.	J. Boulva
W 4754	*M. aeglefinus*	?	5	80	7.5	Feb. 8/35	Off Nova Scotia coast	V. D. Vladykov
W 4740	*M. aeglefinus*	?	5–6	120	22.5	May 27/37	Hackett Cove, N.S.	V. D. Vladykov
W 4743	*G. morhua*	?	5	220	269.0	1935	Off Nova Scotia coast	V. D. Vladykov
W 4768	*G. ogac*	490	4–5	155	69.0	Sept. 18/67	Cambridge Bay, N.W.T.	J. Boulva

[a]Greatest distance between extremities.
[b]Refers to date when specimens were received in Ottawa; date of collection unknown, but probably 1–2 years before.

Melanogrammus aeglefinus — In addition to the typical specimen, W 4754, in Fig. 6, which was in spawning condition, a photograph of the gonads of specimen W 4740 was added. This specimen (details given in Table 1) was taken at the end of the spawning season (maturity stage 5–6). One haddock (440 mm) in the prespawning condition (maturity stage 4–5) was taken south of Halifax, N.S., on December 16, 1970, by P. H. Odense. Two haddock in the same maturity stage, 340 and 470 mm long, were taken east of Newfoundland on March 6, 1971, by A. T. Pinhorn. The gonads of all specimens were of the same morphological type.

Gadus morhua — In addition to the typical specimen, W 4743, in Fig. 7, which was in spawning condition, three Atlantic cod were available. One (630 mm), in prespawning condition, was taken in the Eastern Passage, N.S., during the fall of 1971 by P. H. Odense. Two others (630 and 650 mm), partially spent, were obtained east of Newfoundland on January 25, 1971, by R. Wells. The gonads of all specimens belonged to the same morphological type as W 4743.

Gadus ogac — In addition to the typical specimen, W 4768, in Fig. 8, which was in spawning condition, two more males were available. One (490 mm), in the same spawning condition, was taken at the same place and date as the type. The second specimen, 442 mm long, and in a less advanced stage of maturity (stage 3), was taken from the St. Lawrence River in 1943 by the author (Vladykov 1945). The gonads of all males studied agreed morphologically with the type.

TABLE 2. Types of male gonads, breeding and feeding areas, and maximum length of fish in nine genera of Gadidae.

Scientific name	Type of gonads	Typical habitat		Length (*mm*)	Author
		Breeding area	Feeding area		
		Subfamily *Lotinae*			
Lota lota (Linnaeus 1758)	simple and near-cylindrical without subdivision into lobes	fresh water	fresh water	1000	Nikol'skii (1954)
Urophycis chuss (Walbaum 1792)	irregular lobes, larger in the anterior section than in the posterior section	salt water	salt water	1000	Svetovidov (1948)
		Subfamily *Merlucciinae*			
Merluccius bilinearis (Mitchill 1814)	irregular, short and rather flat convolutions	salt water	salt water	700	Svetovidov (1948)
		Subfamily *Gadinae*			
Microgadus tomcod (Walbaum 1792)	heart-shaped subdivided into a few lobes	fresh water	brackish water[a]	400	Vladykov (1955)
M. proximus (Girard 1854)	heart-shaped subdivided into several lobes	brackish water	brackish water	300	Svetovidov (1948)
Eleginus navaga (Pallas 1811)	heart-shaped subdivided into a few lobes	brackish water	brackish water	320	Nikol'skii (1954)
Boreogadus saida (Lepechin 1774)	cornucopia-like subdivided into several lobes	brackish water	brackish water	360	Nikol'skii (1954)
Arctogadus borisovi Drjagin 1932	several rather short flat convolutions	brackish water	brackish water	600	Nikol'skii (1954)
A. glacialis (Peters 1874)	several rather short flat convolutions	brackish water	brackish water	325	Nielsen and Jensen (1967)
Gadus morhua Linnaeus 1758	many flat convolutions with unindented lobes	salt water	salt water	1800	Svetovidov (1948)
G. ogac Richardson 1836	many flat convolutions with crenate lobes	brackish water	brackish and salt water	490	Vladykov (present study)
Melanogrammus aeglefinus[b] (Linnaeus 1758)	many pipe-like convolutions	salt water	salt water	about 700[b]	Bigelow and Schroeder (1953)

[a]Occasionally it is a permanent resident in fresh water as in the case of the population of Lake St. John, Quebec (Legendre and Lagueux 1948).

[b]Andriashev (1954) reported a single unusually large specimen of 1100 mm.

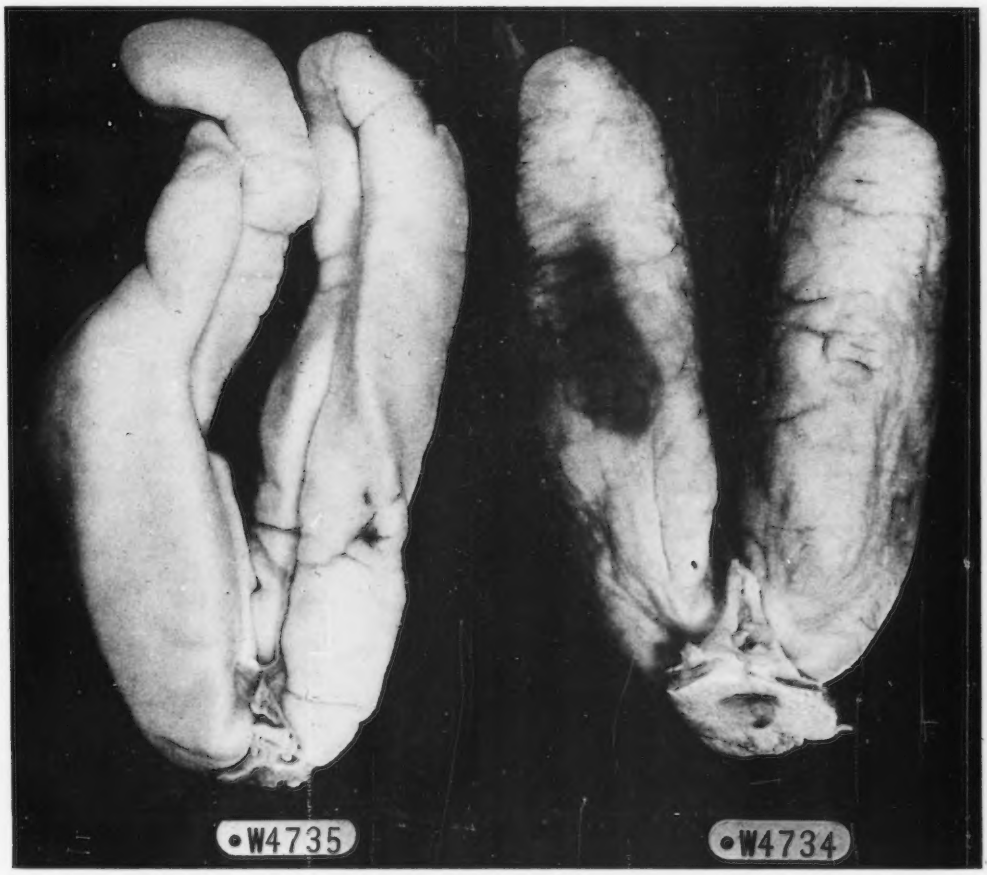

FIG. 1. Nearly mature gonads of burbot (*Lota lota*):
W 4735, testes; W 4734, ovaries.

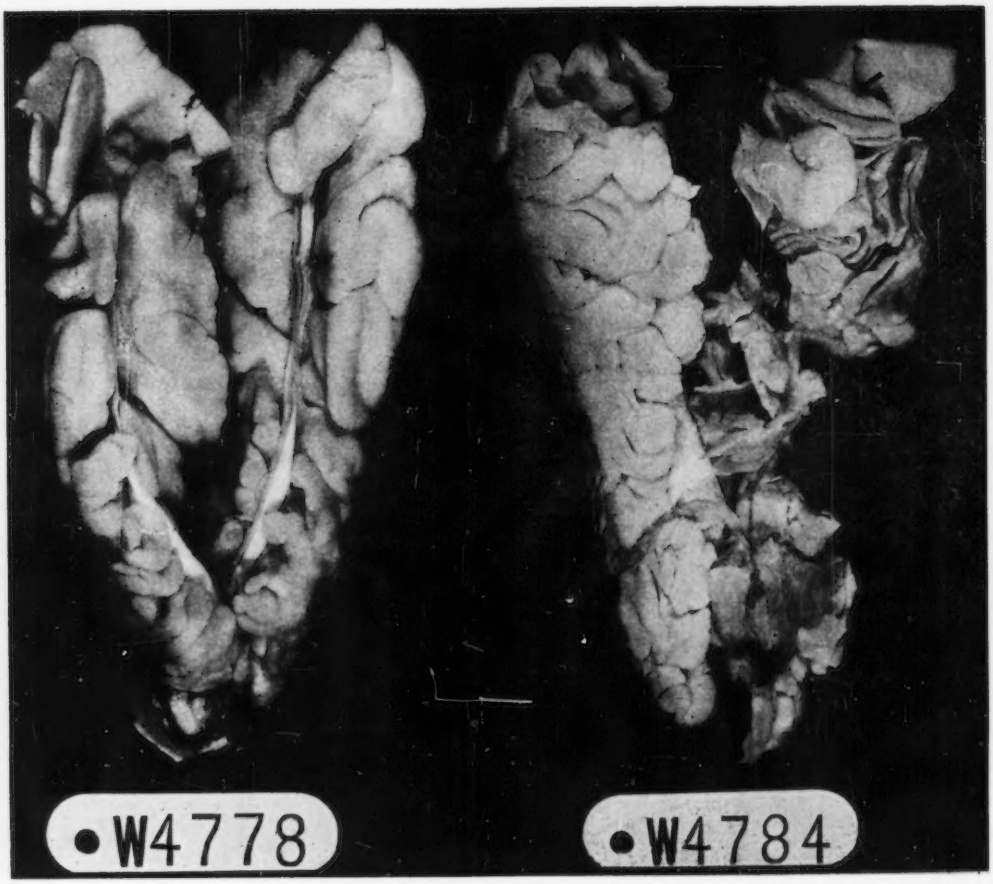

FIG. 2. Mature male gonads of two species of hakes:
W 4778, red hake (*Urophycis chuss*);
W 4784, silver hake (*Merluccius bilinearis*).

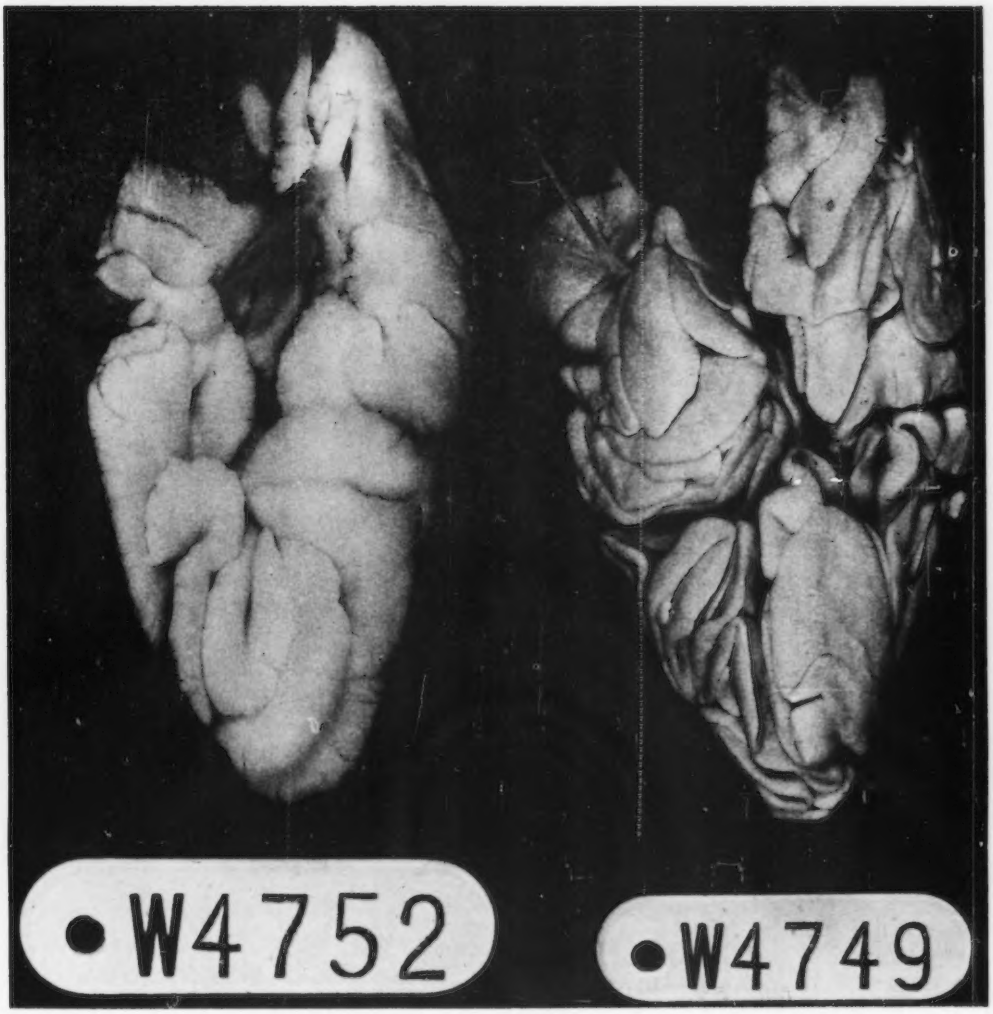

FIG. 3. Mature male gonads of two species of *Microgadus:*
W 4752, Atlantic tomcod (*M. tomcod*);
W 4749, Pacific tomcod (*M. proximus*).

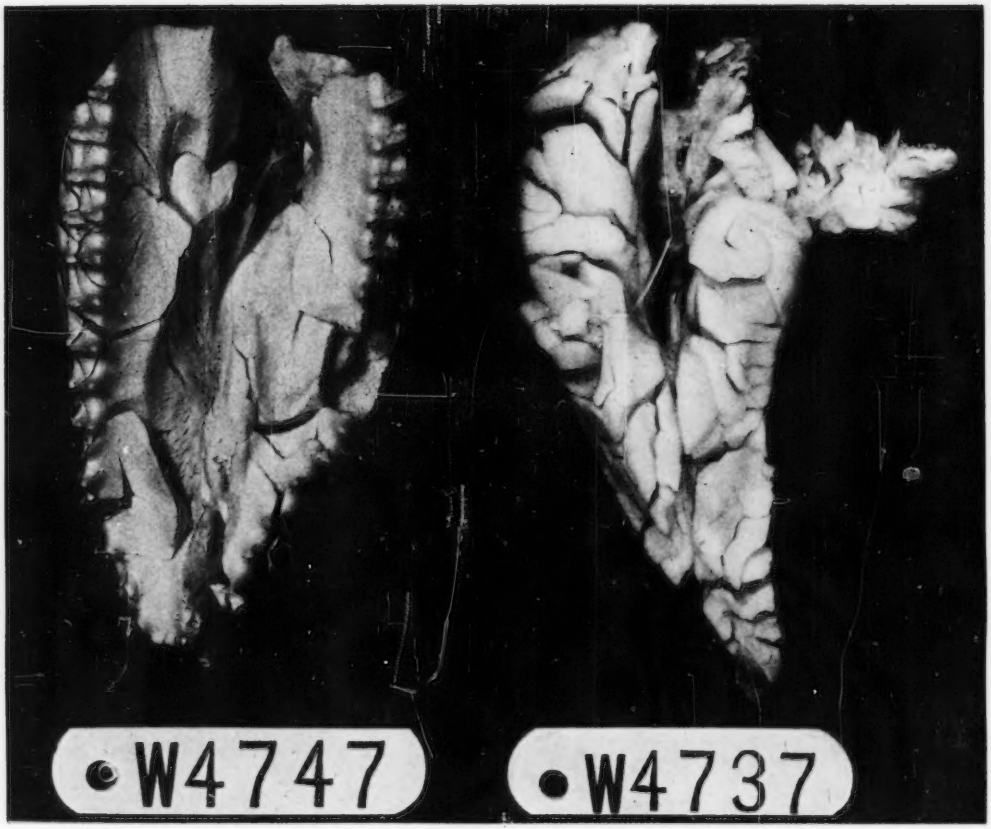

FIG. 4. Mature male gonads of two species:
W 4747, navaga (*Eleginus navaga*);
W 4737, Arctic cod (*Boreogadus saida*).

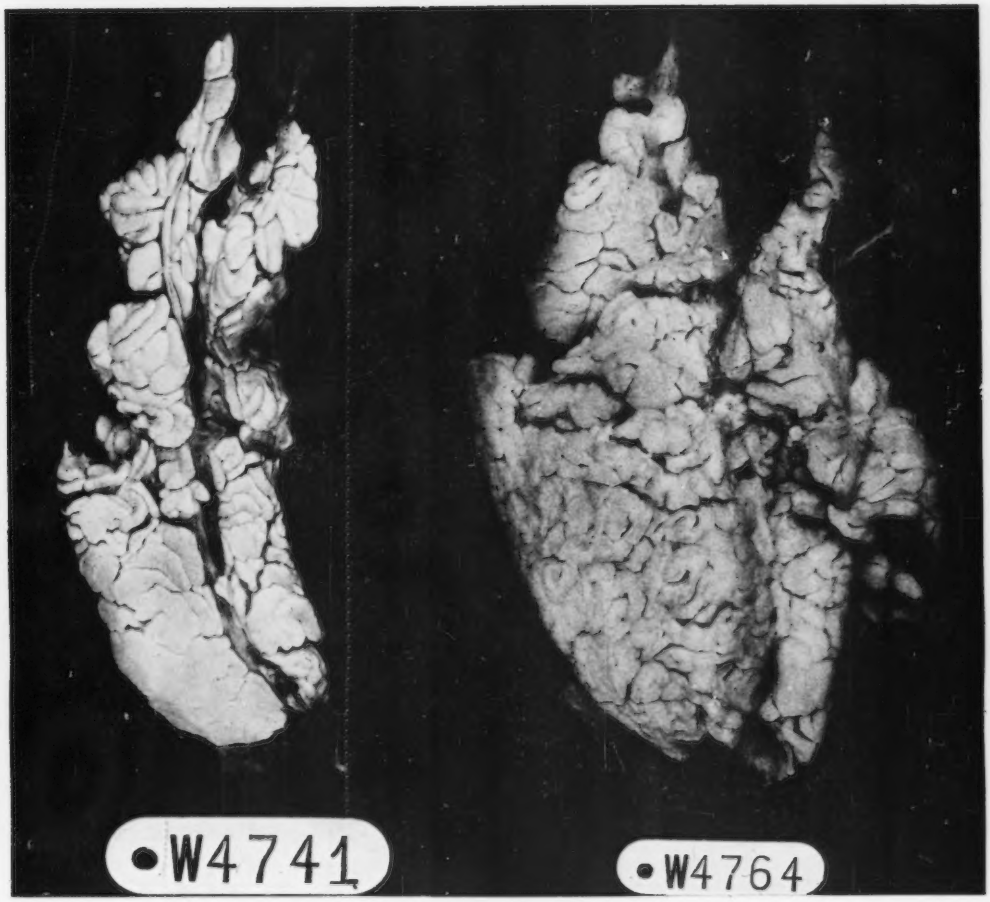

FIG. 5. Nearly mature male gonads of two species of *Arctogadus:*
W 4741, Polar cod (*A. glacialis*);
W 4764, toothed cod (*A. borisovi*).

FIG. 6. Male gonads of haddock (*Melanogrammus aeglefinus*):
W 4754, spawning male;
W 4740, male nearly completed spawning.

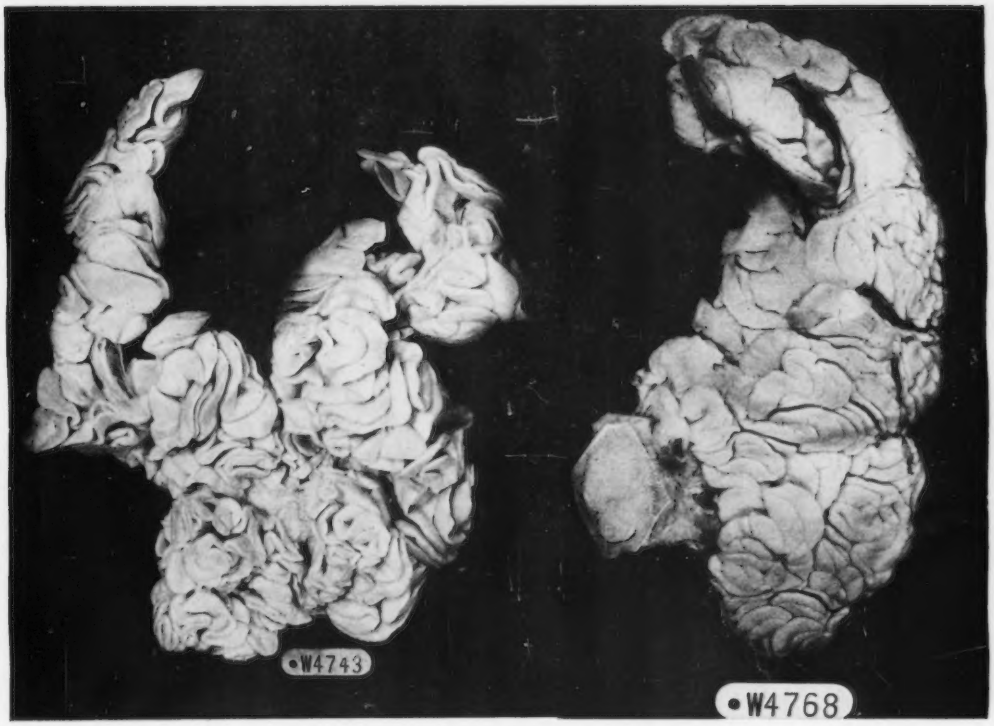

FIG. 7. Mature male gonads of two species of *Gadus:*
W 4743, Atlantic cod (*G. morhua*);
W 4768 Greenland cod (*G. ogac*).

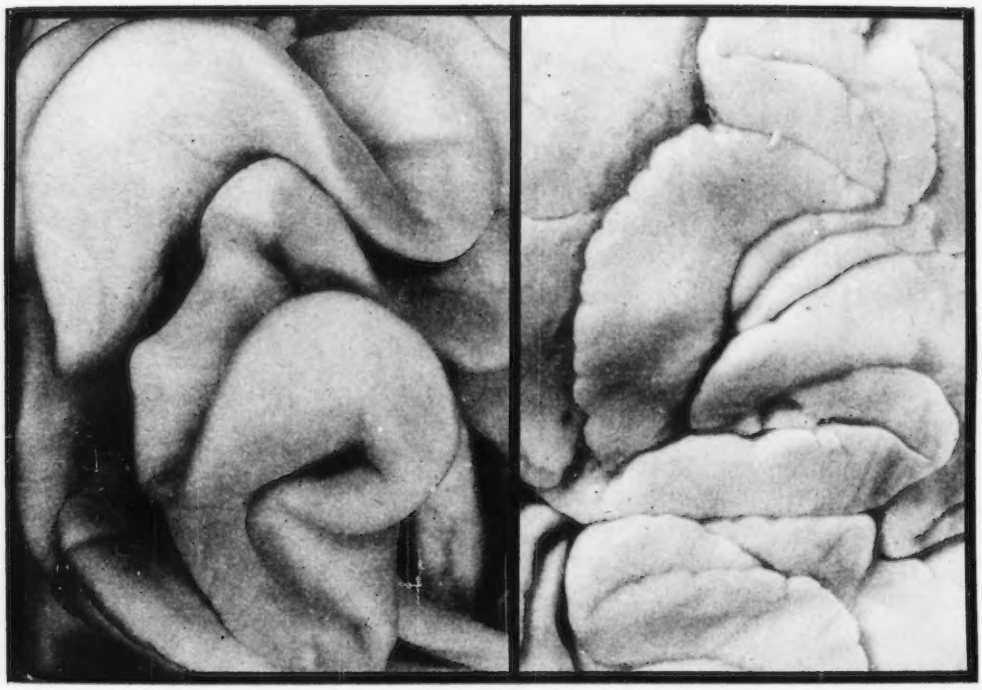

FIG. 8. Sections of male gonads of two species of *Gadus* (the same specimens as those in Fig. 7 but magnified about five times): on the left, *G. morhua* (W 4743), with unindented lobes; on the right, *G. ogac* (W 4768), with crenate ("scalloped") lobes.

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Results

Size of Male Gonads

In general among fishes, the female gonads are heavier than those of the males. For instance, ovaries of a female burbot in prespawning condition (maturity stage 4) were 135 mm long and weighed 169 g. The testes of the same species in a more advanced condition (maturity stage 4–5) measured 145 mm in length and weighed 153 g (Table 1)

Although size of male and female gonads varies with size of fish and stage of maturity, there are, in general terms, three sizes of testes among Gadidae.

The smallest gonads were found among the genera *Microgadus*, *Eleginus*, and *Boreogadus*. The length of their testes varied between 42 and 54 mm and their weight between 4 and 12 g.

In small specimens of *U. chuss* and *M. bilinearis*, the length of testes varied between 42 and 67 mm and weight varied between 9 and 11 g. No doubt, in larger individuals the size of gonads would be much greater.

Among species of *Arctogadus*, only one male, *A. borisovi*, was nearly in spawning condition, and its testes were 110 mm in length and 33 g in weight. The gonads of *A. glacialis* available for this study were not fully developed.

Testes of haddock (*M. aeglefinus*) were available from smaller specimens only and their length varied from 80 to 120 mm and their weight from 8 to 23 g, though the latter figure referred to a partially spent individual. Thus, testes of *Urophycis*, *Merluccius*, *Arctogadus*, and *Melanogrammus* were larger than those of brackish water genera *Microgadus*, *Eleginus*, and *Boreogadus*.

In a mature male *G. ogac*, the testes were 155 mm long and weighed 69 g. The largest male gonads are found in *G. morhua*; in one specimen they measured 220 mm in length and weighed 269 g.

The testes of *Lota* and *Gadus* are the largest in our collection. Histological studies are not completed as yet.

Stages of Maturity in Gadidae

Following earlier experience (Homans and Vladykov 1954; Powles 1958), six stages of maturity in Gadidae were recognized. However, in the early stages, such as 1 and 2, the male gonads are little developed and do not show the characteristic morphological features of spawning fish. The basis for the definition of the four later stages of maturity is taken from Homans and Vladykov (1954). Because the morphological appearance of gonads in different gadid genera varies considerably, only a general definition of the stages of maturity is given.

Stage	*Appearance of gonads*
3	*Early maturity:* the testes begin to develop actively and become whitish in colour but still have rather conspicuous blood vessels. No milt runs when pressure is applied.
4	*Prespawning condition:* the testes are white and quite distended with barely visible blood vessels. Only a few drops of milt can be obtained by pressing.
5	*Spawning condition:* the testes are white and fully distended and the blood vessels are not noticeable. Milt runs freely at the slightest pressure.
6	*Postspawning condition:* the testes are shrunken, and the vasa deferentia are prominent against the irregular surface (Fig. 8, right). Later, the sperm ducts become stringlike.

It is often difficult to assign a gonad to any one stage, so it is assigned to the two nearest stages, as, for instance, 3–4, 4–5, etc..

For a definition of the stages of maturity of females among Gadidae, see Homans and Vladykov (1954) and Powles (1958). Previous to spawning, each ovary looks like an elongated sac full of eggs (Fig. 1, left). The ovaries of spawning fish are distended and often acquire a kidney-shaped appearance The interior structure of ovaries is described in textbooks. The morphological appearance of gadid ovaries does not differ appreciably or at all from one species to another.

Types of Male Gonads

The morphological appearance of testes in different species was characteristic, and showed considerable differences. The available material permitted the recognition of six basic types of testes among Gadidae.

Type I — Each gonad was simple, cylindrical in shape, and not subdivided into lobes. It was found only in *Lota* (Fig. 1).

Type II — The gonads were close together and broader in front, forming a heart-shaped or cornucopia-like structure, subdivided into a few or limited number of lobes. It was observed in *Microgadus* (Fig. 3), *Eleginus*, and *Boreogadus* (Fig. 4). Because each species had distinctions, this type should be subdivided into four sections: *M. tomcod*, IIa; *M. proximus*, IIb; *E. navaga*, IIc; and *B. saida*, IId.

Type III — The gonads were close together and subdivided into irregular lobes. These lobes were larger in the anterior section than in the posterior. This type — IIIa — was found in *Urophycis* (Fig. 2). A modification — IIIb — consisting of short con-

volutions of similar size throughout the gonad characterized *Merluccius* (Fig. 2).

Type IV — The gonads were close together and were subdivided into several rather short and flat convolutions. It was found in *Artcogadus* (Fig. 5). The two species are subdivided into *A. glacialis*, IVa; and *A. borisovi*, IVb.

Type V — The gonads were well separated in the anterior section and consisted of numerous pipelike convolutions. It was found in *Melanogrammus* (Fig. 6).

Type VI — The gonads were clearly separated in the anterior section and consisted of numerous flat convolutions. This type was found in *Gadus* (Fig. 7). The difference between the two common cod species lay in the exterior outline of the lobes. In *G. morhua* (Tag W 4743), the exterior edge of the lobes was unindented (type VIa), while in *G. ogac* (Tag W 4768) the edge was crenate ("scalloped") (type VIb) (Fig. 8).

Discussion

Among different taxa of Gadidae there exists an unusual situation, namely that, among representatives of the same family but of different species, the male gonads are not uniform in structure but greatly varied. In attempting to find an explanation for this morphological diversity, the principal anatomical and physiological peculiarities of Gadidae should first be discussed.

Size of Gadidae

The 12 species of Gadidae studied can be subdivided into three size groups, more specifically, according to their total length (Table 2).

Small species — Representatives of *Eleginus*, *Boreogadus*, and *Microgadus* are smallest, never reaching 500 mm in total length and usually varying from 300 to 400 mm.

Medium species — Total length of the following genera seldom exceeds 900 mm: *Arctogadus*, *Merluccius*, and *Melanogrammus*. In certain areas, haddock (*M. aegelfinus*) may reach up to 1100 mm (Andriashev 1954). Greenland cod (*G. ogac*) should be included among the medium species.

Large species — Species reaching or exceeding 1000 mm in total length include *Lota*, *Urophycis*, and *G. morhua*, the largest species among Gadidae. Giant specimens up to 1800 mm have been reported (Svetovidov 1948).

Fecundity of Gadidae

Gadidae are prolific fishes. Their eggs are less than 2 mm in diameter and, in the majority of species, are free floating (pelagic). The presence or absence of an oil globule in mature eggs characterizes different subfamilies. In Lotinae and Merlucciinae the eggs have an oil globule, while in Gadidae they do not.

On the basis of fecundity Gadidae may be subdivided into three categories:

Species with less than 100 thousand eggs — Includes *Boreogadus*, *Eleginus*, and *Microgadus*, which produce a relatively small number of eggs per spawning. In *E. navaga* and *M. tomcod* the eggs are demersal, while in others they are pelagic.

Species producing between 1 and 2 million eggs — Includes *M. aeglefinus* (Raitt 1933), *G. ogac*, and representatives of *Merluccius* and *Urophycis*. However, information on the last three genera is incomplete.

Species producing more than 3 million eggs — Includes *L. lota* and *G. morhua*. Nikol'skii (1954: 308) reported that a large female *L. lota* can lay up to 5 million eggs per spawning. Svetovidov (1948), Breder and Rosen (1966), and others mention that the maximum number of eggs per spawning for *G. morhua* can reach up to 10 million.

Figures for maximum number of eggs spawned by females of different species refer only to the largest individuals. The smaller females spawn proportionally less eggs.

Authors from Fulton (1881) to Raitt (1933), Bjorn (1941), Powles (1958), and others, when speaking of fecundity of Gadidae, mention only the number of eggs in the ovaries, and pay no attention to the size or morphological peculiarities of the testes.

Spawning Behavior

In Gadidae there is a well-developed swim bladder provided with special drumming muscles which enable the fish to produce sound (Hagman 1921; Jones and Marshall 1953; Templeman and Hodder 1958; Brawn 1961; and Fish and Mowbray 1970). During spawning, sound production plays an important role in courtship. Brawn (1961: 253) stated that in the Atlantic cod (*G. morhua*) "Grunting sounds produced by the male... stimulated the ripe female to respond more effectively to the courtship behaviour of the male. A grunt, with or without a ventral prod by the male, also made a ripe female swim upwards, an action which immediately preceded spawning."

For *M. aeglefinus*, Templeman and Hodder (1958: 355) stated that "male haddock probably use the drumming muscles chiefly to produce low-frequency swim bladder sounds .. in spawning activities."

In spite of a great difference in the systematic position, anatomy, and habitat, spawning of Atlantic cod (*G. morhua*) and burbot (*L. lota*) is similar. Fabricius (1954: 54–55) stated, "In both species one of the fish rests its chin on the crown of its partner, though the upper position is taken by the male in the cod, but normally by the female in the burbot, and in both cases the male in the actual mating act rotates the body so that he turns his back downwards and presses his belly against the female's vent." Contact between male and female during spawning apparently insures efficient fertilization of the numeous eggs that the female gadid produces.

Information on modes of reproduction in other Gadidae is given by Breder and Rosen (1966: 374–384).

Conclusions

Among the 12 species of Gadidae studied, the male gonads can be grouped into six basic types, which correspond to either individual genera or to a group of genera.

It appears that the morphological differences can be associated principally with the type of water (salt or fresh) inhabited and spawning requirements. The freshwater genus *Lota* has simple, nonsubdivided testes, but the marine genera of cold water, *Melanogrammus* and *Gadus*, have complex testes consisting of numerous convolutions. Among genera inhabiting brackish and sometimes fresh water, such as *Microgadus*, *Boreogadus*, and *Eleginus* the testes are subdivided into a small number of lobes. In marine genera *Urophycis* and *Merluccius* of temperate waters, and in the genus *Arctogadus* of Arctic salt and brackish waters, the testes are intermediate in their complexity between the three brackish water genera and the two marine genera.

To understand the morphological peculiarities of male gonads in different species of Gadidae, the study of the development of gonads and their histological structures is essential.

Acknowledgments

Several persons were helpful in the present study. The names of those who collected specimens are mentioned.

Dr A. N. Svetovidov, USSR Academy of Sciences, Leningrad, kindly sent specimens of *E. navaga* from the White Sea. Canadian colleagues of the Fisheries Research Board of Canada, Drs J. G. Hunter, P. H. Odense, and W. Templeman and D. E. McAllister, National Museum of Natural Sciences, Ottawa, provided some marine specimens.

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To all these persons, the author extends his most sincere thanks.

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Size at Maturity, Fecundity, and Embryonic Growth of the Spiny Dogfish (*Squalus acanthias*) in British Columbia Waters

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KETCHEN, K. S. 1972. Size at maturity, fecundity, and embryonic growth of the spiny dogfish (*Squalus acanthias*) in British Columbia waters. J. Fish. Res. Bd. Canada 29: 1717–1723.

Information on the biology of dogfish in British Columbia waters, none of it previously reported, is compared with similar information from other areas of the North Pacific as well as the North Atlantic.

Males and females on both sides of the Pacific have an approximate maximum size of 100 and 130 cm, respectively, or at least 10 cm greater than in the North Atlantic. Females in the North Pacific mature at an average length of 92–100 cm depending on region, as compared to 77–82 cm in the North Atlantic. Males likewise mature at a larger size in the North Pacific.

Observations in Canadian west coast waters show a weak correlation between number of embryos and length of the mother ($r = 0.57$).

Female dogfish produce 2–17 young with an average of 6–7 in the North Pacific off the British Columbia coast; 3–25, averaging 12 in the Sea of Japan; 1–9, averaging 4 in the northwest Atlantic; and 1–10, averaging 3–5 in the northeast Atlantic. Size at birth is about the same throughout the northern hemisphere being between 23 and 30 cm with an average of 25–27 cm.

Intrauterine growth rate is essentially the same in all regions, but at any given time of year differences is size are substantial and are determined largely by differences in time of conception.

KETCHEN, K. S. 1972. Size at maturity, fecundity, and embryonic growth of the spiny dogfish (*Squalus acanthias* L.) in British Columbia waters. J. Fish. Res. Bd. Canada 29: 1717–1723.

L'auteur compare certains aspects inédits de la biologie de l'aiguillat commun des eaux de la Colombie-Britannique avec ceux de la même espèce habitant d'autres régions nordiques du Pacifique et de l'Atlantique.

Sur les deux côtes du Pacifique, le maximum de longueur des mâles et des femelles est de 100 et 130 cm respectivement, soit au moins 10 cm de plus que l'aiguillat de l'Atlantique Nord. Dans le Pacifique Nord, les femelles atteignent la maturité sexuelle à une longueur moyenne de 92 à 100 cm, selon la région, comparativement à 77–82 cm en Atlantique Nord. Les mâles aussi deviennent mûrs à une taille plus grande que dans le Pacifique Nord.

On n'a observé qu'une faible corrélation ($r = 0.57$) entre le nombre d'embryons et la longueur de la mère dans les eaux de la côte ouest canadienne.

L'aiguillat femelle produit de 2 à 17 jeunes, 6 ou 7 en moyenne dans le Pacifique Nord au large de la Colombie-Britannique; de 3 à 25, en moyenne 12, dans la mer du Japon; de 1 à 9, en moyenne 4, dans le nord-ouest de l'Atlantique; et de 1 à 10, en moyenne 3–5, dans le nord-est de l'Atlantique. La longueur à la naissance est sensiblement la même dans tout l'hémisphère nord, soit 23–30 cm, en moyenne 25–27 cm.

Le rythme de croissance intrautérine est essentiellement le même dans toutes les régions, mais il existe, à un moment donné de l'année, des différences considérables de taille, causées en grande partie par le décalage du moment de la conception.

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THE spiny dogfish inhabits temperate coastal waters throughout the northern hemisphere. Although previously the dogfish of the North Pacific was usually regarded as a separate species, *Squalus suckleyi*, Bigelow and Schroeder (1948) could find no morphometric difference between it and *S. acanthias* of the North Atlantic and taxonomists now generally agree that the Pacific spiny dogfish is *S. acanthias*.

The dogfish is of interest to biologists because of its unique reproductive cycle. Ford (1921), in his study of the life history of dogfish of the northeastern

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Atlantic, was the first to discover the long gestation period of almost 2 years. His observations were subsequently confirmed for the northwestern Atlantic by Templeman (1944) and Hisau and Albert (1947); for the northeastern Pacific by Hart (1942) and Bonham et al. (1949); and for the northwestern Pacific by Yamamoto and Kibezaki (1950). These and other authors have presented information on the reproductive features of the dogfish's biology but none make a special point of drawing detailed comparisons among regions of the northern hemisphere. This paper introduces new material for the Pacific coast of Canada and compares observations of maximum size, size at maturity, fecundity, and intrauterine growth rate with findings from other areas.

Materials and Methods

From 1947 to 1968 information on the life history and biology of dogfish in waters off the west coast of Canada was accumulated incidentally to work on other species of groundfish having higher research priority. Since 1969, there have been several opportunities to conduct field studies on dogfish specifically, and these have added substantially to the store of heretofore unpublished data. The present analysis of Canadian data is based on materials collected principally along the east coast of Vancouver Island in the Strait of Georgia. The remainder were obtained from Hecate Strait.

Total length, as referred to in comments on west coast Canadian data, is defined as the distance from the tip of the snout to the tip of the upper lobe of the caudal fin when depressed to align with the longitudinal axis of the fish. Templeman's (1944) measurements were made in the same way, as were those of Bonham et al. (1949). Total length as measured by Japanese investigators apparently is defined as the distance from the tip of the snout to the tip of the upper lobe of the caudal fin in its natural position (Anon. 1956a). The factor for conversion from the "natural" length to the "extended length" is approximately 1.016, which means for any length above 60 cm as measured by the Japanese technique, the converted length is greater by 1 cm or more; for lengths over 123 cm the converted length is greater by 2 cm or more.

Investigators reporting on North Atlantic waters: Ford (1921), Holden and Meadows (1964), and Hisau and Albert (1947); did not indicate which method of measuring was used. However, the resulting differences are not so great as to invalidate the general comparisons made in this paper.

Maximum Length of Adults

Canadian studies of the size composition of Pacific dogfish caught in sunken gillnets (gear selective for large fish) revealed a maximum size of 107 cm for males and 120 cm for females. These observations were made in Hecate Strait and off the west coast of Vancouver Island in 1944 at which time the new and burgeoning fishery for dogfish probably had not affected greatly the primitive size composition. Currently, the usual maximum sizes encountered are about 99 and 124 cm for the two sexes, respectively, but on rare occasions females are found as large as 130 cm. Clemens and Wilby (1961) reported a maximum length of 5 ft 3 inches or 160 cm (undoubtedly a female), but the source of their information is impossible to trace.

Bonham et al. (1949), reporting for areas adjacent to and overlapping waters off the southern coast of British Columbia for 1942–43, gave maxima of 100 and 124 cm for males and females, respectively.

For the northwestern Pacific published data have usually been grouped by 10-cm intervals. The largest males reported by Yamamoto and Kibezaki (1950) from the southwestern portion of the Sea of Japan were in the 100–110 cm size interval, while the largest females were in the 130–140 cm interval. Sato and Inukai (1934), quoted by Anon. (1956a), reported the largest females from the northeastern portion of the Sea of Japan to be in the 130–134 cm interval. In the region between Sakhalin and Peter the Great Bay (northeastern Sea of Japan) Kaganovakaia (1937) noted a maximum size of 126 cm for females. Thus, there appears to be rather little difference in the maximum sizes attained by dogfish of the northeastern and northwestern Pacific.

In the northeastern Atlantic (English Channel), Ford (1921) reported a maximum size of 110 cm for females and 83 cm for males. In the northwestern Atlantic (off Newfoundland), Templeman (1944) reported that the largest dogfish caught during his studies was a female of 108 cm. The largest male was 86 cm. Thus, on both sides of the North Atlantic dogfish appear to reach a smaller maximum size than those of the North Pacific (see Table 1 for summary).

Length at Maturity

Females — On the basis of more than 4300 specimens of female dogfish of 70 cm total length and over, the size at which 50% were mature in waters off the west coast of Canada was 93.5 cm (SD 5.5 cm). The minimum size of maturity was 76 cm (Fig. 1).

In defining "maturity," any female containing uterine eggs or embryos was, of course, so categorized. So also were those whose uteri (actually oviducts) were empty but whose ovaries contained eggs greater than 2.5 cm in diameter or more than half the size of ripe ovarian eggs. (Such a condition is apparent in the early autumn or several months prior to breeding).

The plot of percent mature against length (Fig. 1) shows that so-called immature females are to be

found at least to lengths of 111 cm (one isolated individual was 118 cm long). While such large fish may indeed have remained infertile throughout their life to time of capture, there is a possibility that some females over 100 cm in length were at one time fertile but, depending on time of capture in relation to the breeding season, they had been infertile for at least 2 consecutive years, or would have been infertile for at least 3 consecutive years had they not been caught.

Failure to distinguish sterile females from those which were merely immature over the entire size range above 76 cm, of course, would impart upward

TABLE 1. Comparison of the vital statistics of the spiny dogfish (*Squalus acanthias*) in various regions of the northern hemisphere.

Statistics	Northwest Pacific (Japan Sea)	Northeast Pacific		Northwest Atlantic (Nfld. to Woods Hole)	Northeastern Atlantic (English Chan. and North Sea)
		Bonham	Ketchen		
Breeding season	Apr.–June	Dec.–Jan.	Dec.–Feb.	Feb.–Mar.	Dec.–Mar.
Litter size	3–25	2–17	2–13	1–9	2–15
Average	12	7.3	6.2	4.0	5.4
Birth of young	Feb.–Apr.	Nov.–Dec.	Oct.–Dec.	Oct.–Dec.	Oct.–Dec.
Length at birth	24–30 cm	24–30 cm	23–30 cm	24–31 cm	23–31 cm
Average	26.9 cm	27 cm	26.2 cm	27 cm	27.5 cm
♀ length at maturity (50%)	S. 90–95 cm N. 104–109 cm	92 cm	93.5 cm	77 cm	82 cm
♀ min. length at maturity	<95 cm	78.5 cm	76 cm	74 cm	73 cm
♀ max. length at immaturity	110–114 cm	105.5 cm	118 cm	88 cm	95 cm
Largest female	>130<135 cm	124 cm	130 cm	108 cm	110 cm
Largest male	>100 cm	100 cm	107 cm	86 cm	83 cm

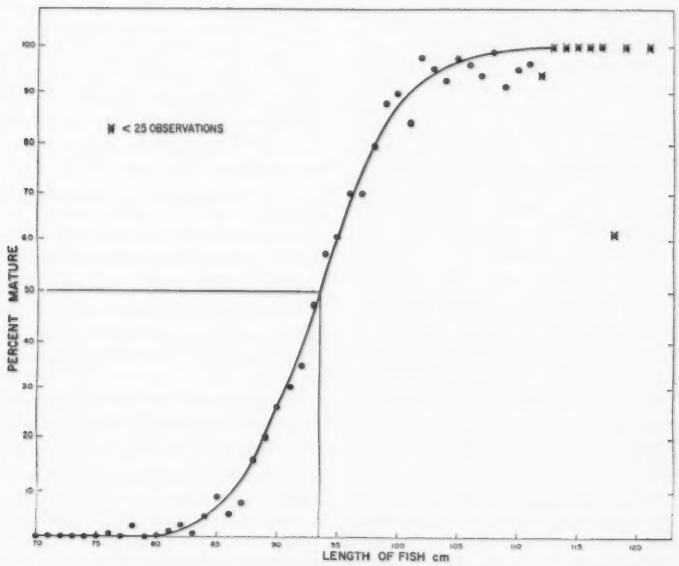

FIG. 1. Relation between the length of female dogfish and percentage maturity, based on observations in British Columbia waters.

bias to the estimate of the 50% point of maturity. However, it is likely that such errors amongst observations of small (76–85 cm) and medium (86–95 cm) females were few in number and hence the bias would be only slight. Actually, amongst the breeding population no instances have been encountered to question the assumption that, once having reached maturity, all females breed every other year.

Table 1 compares estimates of size at maturity as reported by other observers. Bonham et al. (1949), in studies made adjacent to the Canadian west coast, estimated that 50% of the females matured at 92 cm. It is not clear, however, if this was determined from examination of a logistic curve (such as Fig. 1), since 92 cm happens to be the arithmetic mean of the observed minimum size of maturity (78.5 cm) and the observed maximum size of immaturity (105.5 cm).

Observations reported for the southwestern Sea of Japan by Yamamoto and Kibezaki (1950) and Anon. (1956b) suggest that the 50% maturity size for females lies between 90 and 95 cm. However, studies by Sato and Inukai (1934), quoted in Anon. (1956a), suggested a larger size between 104 and 109 cm in the northeastern Sea of Japan (off Hokkaido). Kaganovskaia (1937), referring to the region from the northeastern Sea of Japan to Sakhalin, merely recorded that no females less than 100 cm were found to be mature.

These observations contrast sharply both with those in the northwestern and northeastern Atlantic. Templeman's (1944) analysis of data for the Newfoundland area suggests that the size at 50% maturity is 77 cm, while Holden and Meadows (1964) report a corresponding length of 82 cm in samples from the northern North Sea — 2 cm more than that reported for waters off southern Ireland (Hickling 1930). Thus, it is apparent that the average length of females at maturity is at least 10 cm greater in the North Pacific than in the North Atlantic.

Males — The present study provides no new information on the size of male dogfish at time of maturity. However, the results of a careful study by Bonham et al. (1949) are presumed to be representative of the northeastern Pacific. Examination of the change in size of the claspers (the male intromittent organs) and the presence of appreciable amounts of sperm in the seminal vesicles established fairly clearly a length of 72 cm as the size at which 50% of males reach maturity. Yamamoto and Kibezaki (1950) concluded from studies of the relative growth of testes and claspers that maturity is reached at a size between 70 and 80 cm.

For male dogfish of the northwestern Atlantic, Templeman's (1944) data suggest that 50% maturity is reached at 64 cm. All specimens appeared to be mature at 70 cm. Observations by Hickling (1930) for the northeastern Atlantic led to the conclusion that 50% of male dogfish are mature at a length of 59–60 cm.

Thus, as in the case of female dogfish, the average length of males at maturity appears to be at least 10 cm greater in the North Pacific than in the North Atlantic.

Fecundity

Examination of 190 mature females, ranging from 85 to 118 cm in length (average 98.7 cm), caught in the Strait of Georgia, yielded counts of large ovarian eggs ranging from 2 to 13, with an average of 6.8 eggs per fish. Counts of the number of uterine embryos of 440 pregnant females captured in the same locality at the same time indicated a range of 2–16 per fish, and an average of 6.6 per fish. It should be noted, however, that averages of the number of offspring are rather meaningless unless there is reasonable assurance that the average size of the parents in samples is close to the average for the female parent population as a whole. Generally speaking, in waters off the west coast of Canada pregnant females are greatest in number around 100 cm and at that size the average number of embryos is 6.2 per parent. This approximates conditions in unfished populations.

The relation of size of parent to number of embryos is illustrated in Fig. 2. While the appropriateness of a least squares line of best fit may be debatable, attention is drawn to the variability in numbers of embryos for any given length of parent. The correlation coefficient r is 0.572, and from r^2 we conclude that only 32% of the variability can be attributed to size of parent. An unknown but probably small amount of this variability may be accidental — due to aborting of one or more embryos during the process of being brought aboard by trawl nets.

For an earlier time period in the same general area of the northeastern Pacific, Bonham et al. (1949) reported litter sizes of 2–17 per parent, averaging 7.3.

In respect to the northwestern Pacific, Kaganovskaia (1937) reported a range of 5–19 and an average of 11 embryos for the northeastern Sea of Japan. Japanese investigations indicate a range of 3–25 embryos and an average of 12 (Anon. 1956a). Fecundity in the northwestern Pacific accordingly appears to be substantially greater than in the northeastern Pacific.

In the northwestern Atlantic, Hisau and Albert (1947) observed that the number of large ovarian

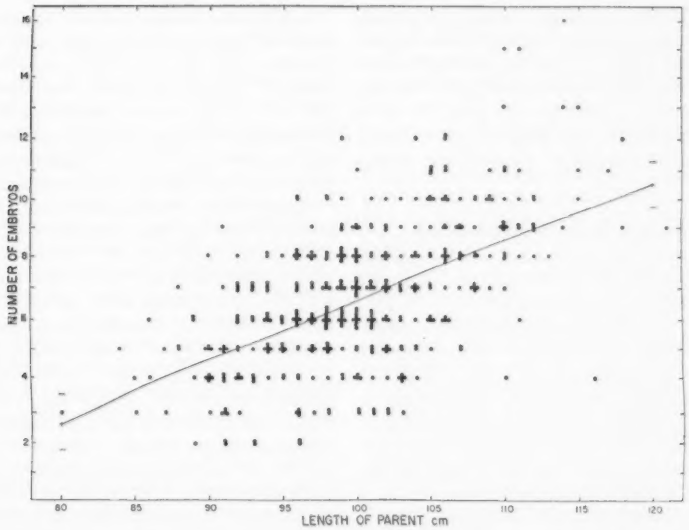

FIG. 2. Fecundity (number of uterine embryos) related to length of female dogfish in British Columbia waters. Regression $Y = 0.20X - 13.24$, where Y is number of embryos and X is length of parent.

eggs was usually 4–6 but never more than 9. Templeman (1944), referring to uterine embryos, noted a range of 1–9 and an average of 4 per parent.

For the northeastern Atlantic, Ford (1921) reported a range of 1 to 10 embryos with an average of 3–5, while Holden and Meadows (1964) showed a range of 2–15 with an average of about 6 per parent. These ranges are more in accord with those for the northeastern Pacific than for the northwestern Atlantic where fecundity is significantly lower.

Conception, Gestation, and Birth

Mature ovarian eggs (3–4 cm in diameter) descend into the shell gland where they are fertilized and pass from there into the oviducts encased in an amber-coloured gelatinous capsule, sometimes referred to as a "candle". The timing of this event cannot be stated precisely. Observations in waters off the Canadian west coast have revealed the presence of encapsuled eggs in the oviducts as early as midNovember and some mature fish still have mature ovarian eggs as late as midFebruary. By midDecember all but a minute fraction of the females not maturing for the first time, or not carrying first-year embryos, have given birth to their young. The time lapse between parturition and refertilization is not known, but it is probable that the breeding season occurs some time in December–February. Bonham et al. (1949) have suggested early December.

In the southwestern Sea of Japan breeding does not seem to occur until April–June, since the birth of young appears to take place from February to April (Anon. 1956a and b, quoting Yamamoto and Kibezaki (1950) and Yusa (MS)).

In the North Atlantic the breeding season is closer to that observed in the northeastern Pacific. Hisau and Albert (1947) concluded that ovulation takes place between February and March, while Ford (1921) suggests the period December–March, and Holden and Meadows (1964) indicate December and January.

As mentioned in the introduction, the dogfish is unique in that the gestation period is nearly 2 years. Most authors assume more specifically that it is somewhere between 20 and 22 months, the indefiniteness being a reflection of the uncertainty of the peak month of liberation of young and the peak month of breeding. It could well be that the average gestation period is as much as 23 months.

In Strait of Georgia waters the birth of young dogfish appears to begin as early as October and is largely completed before the end of November. Bonham et al. (1949) say that birth occurs in November and December, but this seems to be incompatible with their estimate of the time of conception unless, of course, the gestation period is almost 24 months. October–December is suggested as the time of birth in the northeastern Atlantic (Ford 1921), and Octo-

ber–November in the northwestern Atlantic (Hisau and Albert 1947). However, data for the latter region presented by Templeman (1944) suggest that some of the mature dogfish which occur as far north as the Newfoundland coast in summer are likely to give birth later than December. For the stock as a whole, the period October–December is probably more representative.

Embryonic and Fetal Growth Rate

Figure 3 is a composite illustration of the intrauterine growth of dogfish in the northeastern Pacific, based on ranges and averages of sizes determined from both Canadian observations and those of Bonham et al. (1949). By the end of the first year, the average length of embryos is 14–15 cm, at which time they are still wholly dependent for sustenance on a large external yolk sac. By full term the yolk material has been fully absorbed and there remains nothing more than a small umbilical scar.

The exact size of dogfish "pups" at birth is difficult to determine because the observer must assume that those which have completely absorbed their external yolk material are on the verge of liberation and would grow no larger during their remaining time in utero. Also, there may be a time factor, as Ford (1921) has observed that pups of larger than average size are borne by females which give birth late in the season.

Pooled size composition of uterine pups with no external yolk sacs remaining, and sampled during October–December in the Strait of Georgia, ranged from 23 to 30 cm with an average of 26.2 cm (SD = 1.2 cm). Data of Bonham et al. (1949) treated in the same manner indicate a range of 24–30 cm and an average of 25 cm. However, these authors state that the average size at birth is 27 cm.

Nevertheless, estimates of size at birth from all parts of the northern hemisphere are remarkably similar. Whether in the North Pacific or North Atlantic the range of sizes at birth is roughly 24–30 cm, and the average sizes are 26–27 cm (Table 1). What is different, however, is the size of embryonic young at any given month of the year. As might be expected, the curve of growth for embryos in northwestern Pacific waters lags 3–4 months behind that in the northeastern Pacific because of the later breeding season (Anon. 1956a).

Growth rate described by Templeman (1944) and interpreted from data of Hisau and Albert (1947), even though determined from what appears to be one migratory stock along the east coast of North America, must be treated with caution because of seasonal differences in sampling and unavoidable biases induced possibly by the choice of sampling sites (Newfoundland coast and Woods Hole). For example, dogfish which move as far north as Newfoundland may represent a segment of the stock in which embryonic growth is retarded by the colder environ-

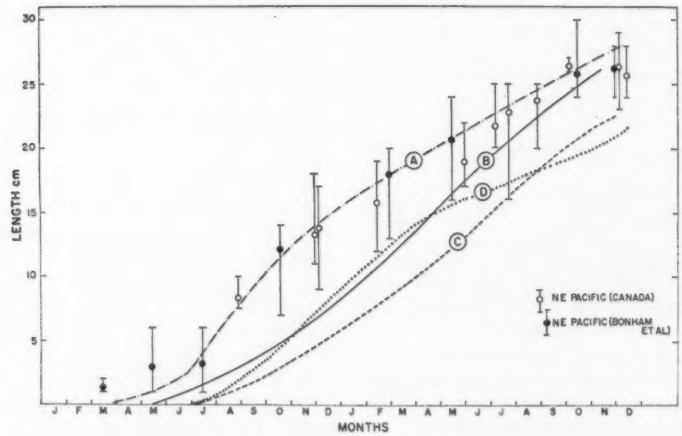

FIG. 3. Mean length and range of lengths of dogfish embryos at various stages of development as observed in the northeastern Pacific and compared with approximate growth curves representing other regions of the northern hemisphere: (A) NE Atlantic (Ford 1921); (B) NW Atlantic (Hisau and Albert 1947); (C) NW Atlantic (Templeman 1944); and (D) Sea of Japan (Yamamoto and Kibezaki 1950).

ment. This is the most likely reason for the different interpolated growth curves shown in Fig. 3 for the northwestern Atlantic.

Applying Templeman's data to Fig. 3, the mean lengths during the July–November period fall well below the lower limits of the range of sizes observed in the northeastern Pacific. The data of Hisau and Albert (1947), collected during the months of May and November as the dogfish migrate northward and then southward, respectively, past Woods Hole, provide estimates of growth in the first year which, like Templeman's data, fall short of the lower limits of the curve for Pacific data. However, their data for November during the second year of pregnancy (near full term) suggest that the lag during the first year is compensated by a more rapid growth in the second year, which leads to a date and size at birth corresponding roughly with observations in the northeastern Pacific.

Data on intrauterine growth of dogfish of the northeastern Atlantic (Ford 1921) follow a pattern almost the same as that demonstrated for the northeastern Pacific.

General Discussion

In the foregoing presentation, several noteworthy biological differences have been revealed among dogfish "populations" of the northern hemisphere. In the first place, whereas dogfish of the North Atlantic and northeastern Pacific give birth to their young in the late fall and winter months and appear to breed during the winter months, these events are delayed until the late winter and spring in the northwestern Pacific. This difference cannot be readily associated with environmental differences among areas since, superficially at least, the temperature domains of dogfish in the Sea of Japan, the northwestern Atlantic, and northern North Sea are not notably different.

Secondly, dogfish of the North Pacific, compared to those of the North Atlantic, are of considerably larger size at first maturity and attain a larger maximum size. These features serve, perhaps, to explain the differences in fecundity — North Pacific dogfish tending to produce larger litters than those of the North Atlantic (with probable exception of the northern North Sea).

The prima facie evidence suggests that dogfish have a faster growth rate in the North Pacific than in the North Atlantic. Surprisingly, the reverse appears to be the case, and this has already been noted by Holden and Meadows (1964). However, it is beyond the intent of this paper to delve into the subject of growth, as this has been reserved for a subsequent paper, again with focus primarily on dogfish of the northeastern Pacific.

Acknowledgments

Numerous members of the Nanaimo Station staff have been involved at one time or another in the collection of data on the biology of the spiny dogfish. To them, and particularly to Mr M. S. Smith, grateful acknowledgment is extended for their valuable assistance.

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Effects of Several Factors on the Growth of the American Lobster (*Homarus americanus*) in Captivity

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McLeese, D. W. 1972. Effects of several factors on the growth of the American lobster (*Homarus americanus*) in captivity. J. Fish. Res. Bd. Canada 29: 1725–1730.

With existing methods, there is little possibility of growing lobsters economically through a moult in captivity.

In initial experiments on effects of temperature, feeding rate, diet, and sex on growth of spring-caught lobsters of 0.6–1.0 lb (0.28–0.45 kg) in captivity, gross weight of all 19 groups decreased by an average of 36% by 6 or 8 months (McLeese 1972).

In these experiments on effects of maturity and storage density, lobsters of 1.0 lb (0.45 kg), maintained at four storage densities at 15 C, were fed fish, squid, and beef liver at 6% of their weight per week. Moulting occurred mainly from early July to late October with only a few others moulting by March (10 months). There was no difference in weight increment for mature and immature lobsters. Mean increments in length and weight were inversely related to storage density. Heavy mortality in one group was caused in part by lobster blood disease, gross weight in the remaining six decreased by an average of 2.5% by 6 months, and 19% by 10 months, corresponding with mortality of 17.5 and 29.4%.

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Les méthodes actuelles n'offrent que peu de possibilité d'élever économiquement des homards et de leur faire traverser une période de mue en captivité.

Au cours d'essais préliminaires sur les effets de la température, du taux d'alimentation, du régime et du sexe sur la croissance en captivité de homards capturés au printemps et pesant de 0.6 à 1.0 livre (0.28–0.45 kg), le poids brut des 19 groupes étudiés diminue de 36% en moyenne après une période de 6 à 8 mois (McLeese 1972).

Au cours des présents essais sur les effets de la maturité et de la densité d'entreposage, des homards de 1.0 livre (0.45 kg), maintenus à quatre différentes densités d'entreposage à 15 C, ont été nourris de poissons, d'encornets et de foie de boeuf, à raison de 6% de leur poids par semaine. La mue se produit surtout du début de juillet à la fin d'octobre, quelques individus muant jusqu'en mars (10 mois). La croissance pondérale des homards matures ne diffère pas de celles des immatures. La croissance moyenne en longueur et en poids est inversement proportionnelle à la densité d'entreposage. Les fortes mortalités subies par un groupe en particulier sont causées en partie par la maladie du sang du homard. Le poids brut des six autres groupes diminue en moyenne de 2.5% au bout de six mois, et de 19% après dix mois, avec mortalités correspondantes de 17.5 et 29.4%.

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In experiments reported here, effects of maturity and storage density on growth of lobsters (*Homarus americanus*) weighing about 1 lb (0.45 kg) were investigated through at least one moult in captivity. Main criteria to assess the experiments were mortality, percentage moulting, time of moulting, length and weight increments per moult, and change in gross weight of groups of lobsters. Also, some consideration was given to moulting frequency and to mutilation, such as claw loss. Factors investigated in initial experiments were temperature, feeding rate, diet, sex, and shelter (McLeese 1972).

In Canada, there are four minimum legal sizes of lobsters, varying from 63.5 to 81.0 mm ($2\frac{1}{2}$–$3\frac{3}{16}$ inches) carapace length (CL), depending on region. Where of legal size, those between 63.5 and 81.0 mm CL are processed into meat. Those measuring 81.0 mm and larger are marketed alive and are usually more valuable per unit weight. By law, fishermen are required to return sublegal-sized lobsters to the fishing grounds. Survival of the released ones is generally considered to be quite

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high, provided they are handled carefully and quickly. However, at different times and places, predators may destroy many of the released ones before they can find adequate shelter (Wilder personal communication). Many sublegal-sized ones are large enough to attain or exceed the minimum size limit for the particular area within one moult (Wilder 1953, 1963).

As an alternate to releasing them, biological and, to some extent, economic aspects of retaining sublegal-sized lobsters until they moult and increase in size were explored in initial experiments and in those reported here. Culture, as reviewed for lobsters (Kensler 1970; Wilder 1971), usually involves rearing animals from the egg to a marketable product. These studies also apply to the final phases of culture.

Review of Initial Experiments

Initial experiments explored the effects of temperature, feeding rate, diet, sex, and shelter on growth of lobsters in captivity (McLeese 1972). Because they provide background information for the present studies, a brief review of the experiments is included here.

Series A — The effects of temperature (12, 17, and 22 C) on the growth of captive spring-caught lobsters at three rates of feeding (herring at 3, 6, and 12% of the lobster's weight per week) were studied. The mean time of moulting was 137 days after June 1. There were no clear indications that temperature or feeding rate affected the percentage moulting or the mean time of moulting. Mean growth increments per moult in the nine groups were relatively small, the maximum being 8% in length and 23% in weight. Growth increments, hemocyte counts, and serum protein values were inversely related to temperature. Serum protein values were directly related to feeding rate. Although other factors may have been involved, these findings indicate that the food did not supply adequate nourishment to support good growth.

Gross weight of the nine groups decreased by 25–77% by 8 months, corresponding with mortality of 32–80%. The minimum loss occurred in the group at 17 C and 6% feeding rate.

Series B — Herring contains thiaminase (Nielands 1947) which may have contributed to the mortality and relatively small weight increments in Series A. Animals from Series A were divided into three groups: one was fed herring; another, cod muscle and beef liver; and the third was starved as a control. Temperature was 17 C and the feeding rate was 6%. At 6 months, mortality was 28% for those fed herring, 18% for those fed cod and liver, and 48% for the starved ones. There was no difference in mean time of moulting among the groups, with average time of moulting being 95 days after February 15. The mean growth per moult in length and weight did not differ in the fed groups. However, after 3 months for those fed cod and liver, mean hemocyte count was 17–19% higher and mean serum protein value 19–23% higher than for those fed herring. These observations and the somewhat better survival indicate that the cod and liver diet is the better of the two. In 6 months, gross weight fell 15% for those fed herring and 9% for those fed cod and liver. Compared with Series A, the fed groups had smaller losses in gross weight, mainly because of lower mortality during a shorter storage period.

Series C — To determine if earlier moulting could be promoted, lobsters were given a variety of treatments: (1) immediate temperature rise (0.5 C/day); (2) delay of 15–35 days before temperature rise initiated; (3) a slow rate of temperature rise (0.3 C/day); and (4) exposure to water in which eyestalkless lobsters were moulting. Final temperature was 20 C, and all groups were fed squid, fish muscle, and beef liver at the 6% rate.

Regardless of treatment, no difference in mean time of moulting between groups could be demonstrated, the average time of moulting being 122 days after June 1. Mean growth increments were 7.2% in length and 24.8% in weight. Gross weight in the six groups decreased by 19–40% by 6 months corresponding with mortality of 28–42%.

The mean growth in weight was better than that for any group in Series A or B, indicating that fish, squid, and liver is a better diet than herring or cod and liver. Other differences between the series, for example, stocks of lobsters, tanks, and shelters may also have contributed to the better growth. Individual shelters in this series, compared with mesh compartments in Series A and B, were more efficient in terms of maintenance such as feeding and cleaning and did not contribute to increase in cannibalism.

In Series A, B, and C mortality was relatively high, moulting appeared to be delayed, and growth per moult was considerably less than expected for lobsters in nature. Consequently, gross weight of all groups decreased appreciably by 6 or 8 months.

Materials and Methods

Mainly to study effects of maturity and storage density on their growth in captivity, hard-shelled lobsters of both sexes from the Gulf of St. Lawrence and Bay of Fundy areas were selected from commercial shipments

as they arrived at a nearby lobster plant in late May of 1965 and 1966. Their mean carapace length was 81 mm (77–89 mm) and mean weight was 440 g (370–528 g). Some in the Gulf stock (1966) were large enough to be mature, those from the Bay of Fundy (1965 and 1966) were immature (Templeman 1936; Wilder 1953). Later observations showed that over 60% of the females from the Gulf became eggbearing during the first 3 months of the experiment.

Each lobster was weighed to the nearest gram after draining for 10 min, carapace length was measured in millimeters, and a numbered monel metal tag was attached to the carapace. Claws not previously inactivated were banded with wide rubber bands (Wilder and McLeese 1961).

Fiberglass tanks (0.9 × 0.9 × 0.3 m), stacked three high, received water from constant temperature header tanks. Temperature taken daily in each tank seldom fluctuated more than ±1 C from 15 C. Salinity, measured weekly, remained within the range 29–32‰. In addition to the water flow, air diffusor stones in each tank provided continuous aeration. Dissolved oxygen, measured weekly, averaged 8 ppm (range 4–10).

Food was squid, fish muscle, and beef liver at the rate of 6% of the lobsters weight per week. They were fed three times a week but only one type of food was presented at a particular feeding. Aluminum shelters, 10 cm × 23 cm, were provided for each individual. Any lobsters that died were replaced to maintain densities.

The experimental arrangement is summarized below:

Density (m^2/*lobster*)	No. lobsters/ tank	No. tanks	Total no. lobsters/ group	Duration of tests (*months*)
0.05	18	3	54	10 June, '65–Mar., '66
0.1	9	6	54	
0.2	5	10.5	54	
0.4	2	7.5	15	
0.05	18	3	54	15 June, '66–Aug., '67
0.05	18	3	54	
0.4	2	27	54	

Length becomes constant within 1 day after the moult (Templeman 1936), and it was measured within 1–7 days postmoult. Intact lobsters were weighed at 8 weeks postmoult to obtain their final weight (McLeese 1972). Data for growth increments following a moult were analyzed, using the analysis of variance for samples of unequal size (Steel and Torrie 1960; Goulden 1952). Times to 50% moulting and 95% confidence limits were obtained from plots of percentage moulting against time on logarithmic-probability paper (Litchfield 1949). The times were expressed as number of days after June 1.

Results

Mortality

One group of lobsters had a mortality of 70% at 6 months (Table 1), caused largely by the blood disease gaffkaemia (Snieszko and Taylor 1947), apparently introduced with lobsters added to maintain density. Examination of blood smears (Wilder and McLeese 1961) showed that 22 of 29 lobsters that died during the 5th and 6th months were infected with *Gaffkya homari*. In the remaining six groups, the mortality range was 11–35% at 6 months and 11–45% at 10 months. In two groups observed for 15 months, mortality between 10 and 15 months rose from 25 to 57% in one, and from 45 to 75% in the other, associated largely with renewed moulting either for the first or second time in captivity.

Moulting

Moulting began in early July and continued until late October when 54–100% of the animals had moulted for the first time in captivity (Table 1). Little further moulting occurred by March (10

TABLE 1. Summary of mortality, moulting, and gross weight change for lobsters at 15 C (0.05–0.4 m^2/lobster) fed fish, squid, and beef liver at 6% of the lobster's weight/week.

Year	Experimental conditions: Density (m^2/*lobster*)	Maturity	Mortality at (*months*): 6 (%)	10 (%)	15 (%)	Moulting[a] at (*months*): 6 (%)	10 (%)	15 (%)	Days to 50% moulting after June 1 and 95% confidence limits	Gross weight change in 6 months (%)
1965	0.05	I	11	39	–	93	93(4)	–	122±5	+1.4
	0.1	I	35	43	–	80	80(4)	–	127±7	–14.6
	0.2	I	11	15	–	95	95(6)	–	119±5	+5.5
	0.4[b]	I	13	13	–	100	100	–	109±13	+11.9
1966	0.05	M	20	45	75	54	59	76(7)	149±20	–9.2
	0.05	I	70	–	–	95	–	–	112±8	–
	0.4	I	15	25	57	69	72	87(37)	122±16	+1.0

[a] % moulting for second time in parentheses.
[b] 15 lobsters in this group, 54 in others.

months). In the two groups observed beyond 10 months, 15 and 17% moulted for the first time and 7 and 37% for the second time, mostly between 11 and 14 months.

Time to 50% moulting for the six groups of immature lobsters ranged from 109 to 127 days after June 1 (average 120 days) and the times were not different. The time for the mature group, 149 days after June 1, was significantly later ($P < .05$). Sixteen of the 26 females became eggbearing during the first 3 months of the experiment. Mainly because these could not moult until after the larvae hatched, only 59% of the group had moulted by 10 months.

Growth Increments

In the 1965 and 1966 data, mean increments in length and weight per moult increased as storage density decreased (Table 2), and the effect was significant in both sets of data ($P < .001$, Table 3). The two largest individual increments, 56.3% for an 83 mm CL male (1965 data) and 55.1% for an 87 mm CL female (1966 data), occurred at 0.4 m^2/lobster and were as large as those expected for lobsters in nature.

At 0.05 m^2/lobster, mature lobsters had smaller length increments than immature ones; however, the mean weight increments were similar (Table 2). Females in the 1965 data had larger length in-

Table 2. Summary of lobster length and weight increments following a moult.

Year	Experimental conditions: Density (m^2/lobster)	Maturity	Length increment: Males No.	Males Mean	Males SE	Females No.	Females Mean	Females SE	Total No.	Total Mean	Total SE
1965	0.05	I	18	8.5	.35	25	9.1	.40	43	8.9	.27
	0.1	I	14	7.9	.53	13	10.4	.71	27	9.1	.49
	0.2	I	23	9.6	.46	23	10.6	.47	46	10.1	.33
	0.4	I	5	11.7	.26	8	11.9	.52	13	11.8	.33
1966	0.05	M	22	7.4	.33	13	6.4	.31	35	7.0	.25
	0.05	I	20	8.5	.36	26	8.5	.35	46	8.5	.25
	0.4	I	21	10.4	.49	22	10.6	.57	43	10.5	.37
						Weight increment					
1965	0.05	I	14	29.0	1.9	22	29.4	1.6	36	29.2	1.2
	0.1	I	7	27.3	2.7	9	36.5	2.3	16	32.5	2.0
	0.2	I	13	31.9	2.0	16	34.4	1.7	29	33.3	1.3
	0.4	I	2	48.5	7.9	4	40.8	1.8	6	43.3	2.8
1966	0.05	M	15	32.6	2.7	6	23.4	2.3	21	29.9	2.2
	0.05	I	11	28.0	1.1	13	29.4	2.1	24	28.7	1.2
	0.4	I	11	40.2	2.7	15	37.4	2.3	26	38.6	1.7

Table 3. Analysis of variance for length and weight increments for 1965 and 1966 experiments.

Year	Source of variation	Length increment DF	Length increment MS	Length increment F	Weight increment DF	Weight increment MS	Weight increment F
1965	Density	3	33.52	8.1[a]	3	365.95	7.1[a]
	Sex	1	28.15	6.8[b]	1	15.96	0.3
	Interaction	3	6.42	1.6	3	116.55	2.3
	Error	121	4.14	–	79	51.43	–
1966	Density	2	122.46	28.4[a]	2	849.49	12.6[a]
	Sex	1	2.30	0.5	1	192.85	2.8
	Interaction	2	3.44	0.8	2	139.47	2.1
	Error	118	4.31	–	65	67.50	–

[a]Significant .001 level.
[b]Significant .01 level.

crements than males ($P < .01$), but there was no difference in their weight increments. Length and weight increments did not differ with sex in the 1966 data (Table 3).

Gross Weight

Gross weight of each of the seven groups, expressed as a percentage of initial weight, was measured at 6 months (Table 1). In four of the seven groups, gross weight increased by an average of 2.5% (1.0–11.9%). For these, mortality averaged 12.4%; moulting, 86.5%; and mean weight increase, 33.8%. By 10 months, additional mortality, with little new moulting, lowered the average gross weight, the loss averaging 12% of the initial weight. In two groups, gross weight at 6 months averaged 12% (9.2–14.6%) less than the initial weight and, by 10 months, it was about 30% less than the initial weight. The remaining group, with a mortality of 70% at 6 months, had a loss in gross weight of 62%.

Claws (chelipeds) comprise 34% of the live weight of 1 lb (454 g) lobsters (McLeese 1972). Of 249 lobsters alive at 6 months, 18 had lost a "pincer" claw, 35 a "crusher" claw, and 9 had lost both. In other words, 71 (14.2%) of the claws were missing, resulting in an estimated weight reduction of 4.8%.

Discussion and Conclusions

Whether a lobster dies before or after moulting, its initial value is lost. However, to develop methods to reduce mortality, it is important to know whether deaths of moulted or nonmoulted ones cause most of the mortality. Obviously, early deaths are likely to be of nonmoulted lobsters and, as moulting increases with time, later deaths are likely to be of moulted ones. Excluding those in the group with blood disease, 52 animals died by 6 months. Of these, 15% died before moulting, 58% died 0–7 days postmoult, and 27% between 1 and 12 weeks postmoult. Provided the main cause of death of moulted ones is related to interaction with other lobsters, segregation of those about to moult, until a week postmoult, might eliminate up to about 60% of the mortality. Moulting at the maximum rate in the various groups ranged up to 16% of the animals per week. Accordingly, additional tank space, sufficient to house 16% of the animals temporarily, would be required for segregation. To be economically practical, the value of any saved ones must exceed costs for temporary segregation.

Significant differences in time of moulting related to storage temperature, diet, or other factors could not be demonstrated in initial experiments (McLeese 1972). Hughes and Matthiessen (1962) found that moulting activity was greatest in the 15–20 C range and was reduced at temperatures exceeding 20 C when average monthly temperature varied seasonally from about 2 to 23 C. However, later work at essentially constant temperatures indicated that lobsters moult more frequently at an average temperature of 23.9 C than at 21.3 C (Hughes personal communication).

Templeman (1936) concluded that lobsters of about 25–70 mm CL in the Northumberland Strait may moult in July and again in September. Wilder (1963) reported that 95 of 110 marked ones (about 56–62 mm CL) from that area had moulted for the second time by October 5. Similar sized ones (63–75 mm CL) from that area were impounded in late May for initial Series A. However, not more than 0–14% moulted by the end of July and only 10 (2.2%) moulted for the second time by February, although maintained at constant temperatures from 12 to 22 C (McLeese 1972). Slightly larger mature ones (Table 1), also from that area, had only 7% moulting for the second time by 15 months. The different moulting patterns for lobsters in nature and those in captivity may have been influenced by the sizes of the lobsters and, possibly, by natural variations in moulting time in different years. However, it seems likely that conditions in captivity contributed to the apparent delay in moulting. Delay in initial moulting necessitates longer storage, increases the chance for losses from deaths and mutilations, and increases maintenance costs. Also, the possibility of moulting for a second time within a reasonable period is reduced.

Growth per moult was shown to be greater at the lower storage densities. The exact nature of the space effect is not known. Since water depth in the tanks was uniform, it is assumed the effect is related to floor area. At the lowest storage density mean weight increment was 39.4% (combined data, Table 2). A few individuals grew 55–56% in weight, as much as expected for lobsters in nature. Whether reducing the storage density further would allow more individuals to achieve maximum growth, thereby increasing the mean growth, was not tested.

In initial experiments fish, squid, and liver produced better weight increments than herring or cod. It was pointed out that differences other than diet may have contributed to the better growth. Except for temperature, methods were the same for lobsters at 0.05 m^2/lobster in these experiments and in initial Series C. Mean weight increases of 28.7–29.9% at 15 C in these experiments were larger than 24.8% at 20 C in Series C. Apparently, the food, the rate, or the frequency of feeding or a combination of these factors did not supply enough nourishment to maintain good growth at the higher temperature.

To improve growth, further change in diet as well as change in the amount fed and frequency of feeding (e.g. daily feeding versus three times a week) are reasonable possibilities. Providing space of 0.4 m^2 or more per lobster may not be practical for large-scale culture operations since capital costs to house large numbers of lobsters are likely to be excessive. If the storage density effect is related mainly to floor area, relatively deep tanks with trays could be used to reduce capital costs. Alternately, intermediate space could be used, the lower storage costs tending to offset the smaller growth per moult.

Relatively low cost storage, for example, in tidal ponds from which lobsters are sold before they moult and grow, is profitable at certain seasons because market value increases when landings are low or when freshly caught ones are soft-shelled and difficult to store and ship (McLeese and Wilder 1964). Growing them in captivity will provide additional profit if their final value exceeds their appreciated initial value and additional costs associated with their culture.

Results for a group of lobsters at a particular time, as judged by gain or loss in gross weight, depend on growth per moult, number that moult, number that die, and weight loss from mutilations among the survivors. Only four of the seven groups showed slight gains in gross weight by 6 months, with all showing a loss by 10 months. Weight reduction from loss of claws was estimated to be about 4.8%. In addition to the loss in weight, one-clawed lobsters are less valuable per unit weight. Those without claws are almost worthless. Consequently, gross weight cannot be converted directly into "value" without accounting for the reduced values per unit weight for any missing one or both claws. By 6 months, 21% of the survivors had lost one, and 3.6% had lost both claws.

With little possibility of gain in gross weight, increase in value for a group depends on the lobsters attaining a more valuable size. Based on records for Miminegash, Prince Edward Island, from 1968 to 1970, landed value of lobsters 81 mm CL and over averaged 25% (15–33%) more per unit weight than for the smaller legal-sized ones. The larger ones are marketed alive at values exceeding their landed value, whereas the smaller ones are processed into meat soon after capture. As mentioned previously, only a few animals moulted twice by 10 months. Consequently, with an average increase in length of 10.8% (0.4 m^2/lobster, Table 2), only those between 73 and 81 mm CL could be expected to grow enough in 10 months to attain the more valuable size.

It is unlikely to be economically feasible to grow lobsters in captivity quickly to more valuable sizes, either as an alternate to releasing them on the fishing grounds or for commercial culture, until methods to virtually eliminate mortality and mutilations are developed. Also, there remains the need to find diet, feeding frequency and rate, and storage density, among other factors, that will promote maximum growth per moult at high temperatures where maximum moulting frequency should occur.

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Use of a Commercial Dredge to Estimate a Hardshell Clam Population by Stratified Random Sampling

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RUSSELL, H. J., JR. 1972. Use of a commercial dredge to estimate a hardshell clam population by stratified random sampling. J. Fish. Res. Bd. Canada 29: 1731–1735.

With stratified random sampling, use of a commercial dredge provided a valid estimate of the population of the hardshell clam *Mercenaria mercenaria* in Narragansett Bay, Rhode Island. Because of the nonrandom distribution pattern of *M. mercenaria*, treatment of the data with normal statistics would indicate a mean of 1.64 bu per dredge tow with a variance of 1.80. Stratified sampling, due to its inherent weighting feature, provided a similar estimate of 1.36 bu per tow with a variance of 0.033.

RUSSELL, H. J., JR. 1972. Use of a commercial dredge to estimate a hardshell clam population by stratified random sampling. J. Fish. Res. Bd. Canada 29: 1731–1735.

Tel qu'appliqué dans cette étude, le procédé statistique d'un échantillonnage stratifié pris au hasard nous a permis l'emploi d'une drague commerciale pour obtenir un estimé valide d'une population de *Mercenaria mercenaria*. Le hasard n'étant pas la norme de distribution de *M. mercenaria*, un traitement statistique normal des données indiquerait une moyenne de 1.64 boisseaux par coup de drague avec une variance de 1.80. Un échantillonnage stratifié, à cause du facteur pondérant qui lui est inhérent, fournit une évaluation semblable de 1.36 boisseaux par trait, avec une variance de 0.033.

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SURVEYS of marine bivalve molluscs of Narragansett Bay, Rhode Island, conducted with the view of providing population estimates intended for management decisions, have in their data analyses largely assumed random distribution of the animals. It is not inconceivable that past work in other areas made a similar faulty assumption.

It has been demonstrated by Saila et al. (1965) that the hard shell clam *Mercenaria mercenaria* occurs naturally in a superdispersed or contagious spatial arrangement described by the negative binomial distribution. However, their data indicate that samples collected with a rocking-chair dredge, instead of a grab sampler, exhibit normality. This suggests that the cells of contagion are relatively small scale and that a dredge acts as an integrating device. Unfortunately, they were unable to satisfactorily evaluate the efficiency of the dredge. In a study of distribution and population estimation of several species of marine bivalves including *M. mercenaria*, Saila and Gaucher (1966) took the approach of normalizing random data collected with a grab sampler so as to allow treatment by normal statistics. The essential requirements were that a large number of samples be taken with strict adherence to a random sampling scheme. In resource surveys the former requirement may constitute a distinct disadvantage.

This paper presents results of the application of a Fall River rocking-chair dredge in a stratified random sampling design in which a limited number of samples sufficed to provide a reasonably accurate population estimate of *M. mercenaria*.

Materials and Methods

SAMPLING DESIGN

As in the case of sequential sampling proposed by Saila et al. (1965), stratified random sampling does not involve the taking of a predetermined number of replicate samples. Instead, both the total number of samples and their locations are influenced by results of a preliminary reconnaissance. The technique may best be understood by visualizing a topographic contour map with peaks representing centers of abundance of animals. The preliminary dredge survey serves to identify centers of abundance and provide the information necessary to construct contours enclosing areas of equal abundance. Subsequent sampling is then directed towards approaching equal sampling fractions based on areas between contours, or strata. The statistical analysis is simplified

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if the sampling fractions are equal but exact parity is not critical to the method.

Evaluation of Dredge Efficiency

Evaluation of the efficiency of the rocking-chair dredge was the necessary preliminary step since a sample must be definable in terms of area.

As the name implies, this dredge rocks back and forth on the skid pads, alternately withdrawing the teeth from the sediment to an extent which is dependent upon characteristics of the substrate. Experienced dredge boat captains are able to make subtle distinctions regarding the degree of "hardness" of the bottom. The dredge does, however, take consistent replicate samples when operated in relatively uniform substrates (Saila et al. 1965).

Advantage was taken of the fact that a commercial dredge season was held in the lower West Passage of Narragansett Bay. The dredge grounds, comprising an area of 520 acres delineated by the 6- and 40-ft depth contours, are predominately silty sand with a variable broken shell and rock constituency. (Fig. 1) This acreage represents only that portion of the Passage in which dredge boats were observed working. A total of 10,925 bu of *M. mercenaria* (874,000 lbs) were harvested.

Both before and after the commercial season a dredge survey was conducted in a manner in keeping with the requirements of stratified random sampling as outlined. Only that portion of each survey corresponding with the commercial dredge grounds will be considered. Each 10-min dredge tow was made as uniform as possible with respect to boat speed and wire angle of the towing warp. Results of the dredge hauls in 80-lb bushels were plotted on overlays of USC&GS Chart No. 236 at their appropriate positions and, where amenable, contours of equal abundance were constructed (Fig. 1). Areas between contours were then computed with a planimeter and a mean catch was assigned to the given area.

The area effectively fished by the dredge during a standard tow was calculated in the form of the number of such tows required to effectively fish an acre.

Let:

T = number of tows per acre
a_i = area in acres of area i of the initial survey
a_j = area in acres of area j of the final survey
b_i = mean bushels per tow in area i of the initial survey
b_j = mean bushels per tow in area j of the final survey

Hence:

$a_i b_i T$ = initial population in bushels in area i (1)
$a_j b_j T$ = final population in bushels in area j (2)

And:

$$\sum_{i=1}^{m} a_i = \text{total area in the initial survey where } i = 1,2,3 \ldots m \text{ individual areas} \quad (3)$$

$$\sum_{j=1}^{n} a_j = \text{total area in the final survey where } j = 1,2,3 \ldots n \text{ individual areas.} \quad (4)$$

Of course (3) equals (4) or 520 acres. However, $m \neq n$ and, hence, the reason for the difference in notation. Combining (1) with (3) and (2) with (4), we see:

$$\sum_{i=1}^{m} a_i b_i T = \text{total initial population in bushels,} \quad (5)$$

$$\sum_{j=1}^{n} a_j b_j T = \text{total final population in bushels.} \quad (6)$$

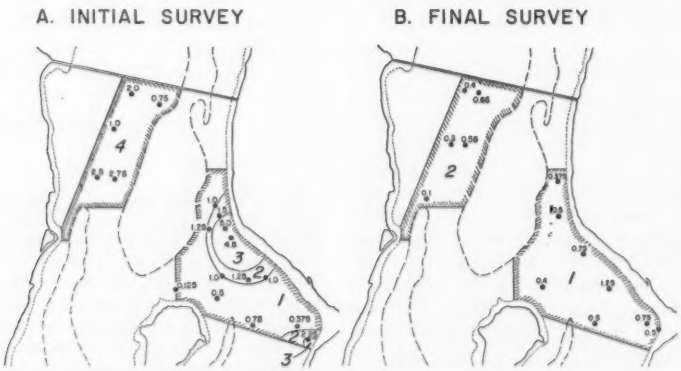

FIG. 1. West Passage dredge grounds. Initial survey (A), final survey (B). Hatching indicates the east shore and west shore areas. Dredge tows in the two surveys with their yields in 80-lb bushels are located and were used to interpolate positions of contours. The 6- and 40-ft depth contours are shown by dots and dashes, respectively.

Evaluation of (5) and (6) in terms of the unknown T was accomplished by summing the individual products a_ib_i and a_jb_j, respectively:

i	a_i	b_i	a_ib_iT
1	222.81	0.44	98.04 T
2	49.61	1.17	58.04 T
3	50.25	3.92	196.98 T
4	197.81	1.80	356.06 T
	520.48		709.12 T

j	a_j	b_j	a_jb_jT
1	322.67	0.63	203.28 T
2	197.81	0.40	79.12 T
	520.48		280.40 T

The difference between (5) and (6) is:

$$\sum_{i=1}^{m} a_ib_i\mathrm{T} - \sum_{j=1}^{n} a_jb_j\mathrm{T} = 10{,}925 \text{ bu} \qquad (7)$$

and after substitution:

$$709.12\ \mathrm{T} - 280.40\ \mathrm{T} = 10{,}925$$
$$\mathrm{T} = 25.6 \text{ tows per acre.}$$

It is evident, therefore, that during a standard 10 min tow the dredge effectively fished a mean area of 1702 ft². No attempt was made to evaluate confidence limits by replicating station tows. However, results by Saila et al. (1965) suggest limits of approximately ± 10% at $P = 0.1$.

It should be emphasized that this technique for estimating the area actually fished by the dredge during a standard tow does not have as an essential requirement the activity of an entire dredge fleet. Thus, comparing catches from several replicate tows made both before and after the same or similar area had a known number of *M. mercenaria* removed by the survey vessel would provide the information needed to calculate a similar estimate.

Population Estimate From Stratified Survey Data

For application of stratified random sampling in this study, strata were defined as areas of relatively uniform abundance of *M. mercenaria* as indicated by results of the two dredge surveys. The total area of each stratum was estimated from a chart while the sampling unit, the individual dredge tow, was also estimated in terms of area. The mathematical procedure expresses the area of a stratum in terms of the total possible contained number of sampling units.

The following notation is after Cochran (1963):

N_h = total number of tows in stratum h
n_h = number of sampling tows in stratum h
y_{hi} = number of bushels obtained in the ith tow in stratum h.

Hence, mean bushels per tow in stratum h is:

$$\bar{y}_h = \frac{1}{n_h} \sum_{i=1}^{n_h} y_{hi}$$

and mean bushels per tow for all strata combined or the weighted sample mean is:

$$\bar{y}_{st} = \frac{1}{\mathrm{N}} \sum_{h=1}^{\mathrm{L}} \mathrm{N}_h\bar{y}_h$$

where L is equivalent to the number of strata and $\mathrm{N} = \mathrm{N}_1 + \mathrm{N}_2 \ldots + \mathrm{N}_\mathrm{L}$.

The variance of the estimate $\bar{y}_{st}$ where the sampling fractions n_h/N_h are negligible in all strata, as in this case, is given by:

$$s^2(\bar{y}_{st}) = \frac{1}{\mathrm{N}^2} \sum_{h=1}^{\mathrm{L}} \frac{\mathrm{N}_h^2 s_h^2}{n_h}$$

where the s_h^2 are the sample variances for the individual strata calculated in the usual manner.

If the n_h are significant fractions of their respective N_h, then finite population corrections must be used so that:

$$s^2_{(\bar{y}_{st})} = \frac{1}{\mathrm{N}^2} \sum_{h=1}^{\mathrm{L}} \mathrm{N}_h\,(\mathrm{N}_h - n_h)\,\frac{s_h^2}{n_h}.$$

Formulae for confidence limits are in the familiar form of:

Population mean: $\bar{y}_{st} \pm t\ s_{(\bar{y}_{st})}$
Population total: $\mathrm{N}\,\bar{y}_{st} \pm t\ \mathrm{N}\ s_{(\bar{y}_{st})}$

where the value of t is from tables of "students" t.

The effective number of degrees of freedom is:

$$n_e = \frac{(\sum g_h s_h^2)^2}{\sum \frac{g_h^2 s_h^4}{n_h - 1}}$$

where $g_h = \frac{1}{n_h}\,\mathrm{N}_h\,(\mathrm{N}_h - n_h)$

The initial population of *M. mercenaria* and that following the dredge season were estimated as 18,148 ± 5704 and 7235 ± 2167 80-lb bu, respectively, at $P = 0.05$ (Table 1). The sample variances for individual strata (with the possible exception of stratum 3 in the initial survey), when compared with their respective sample means, are low enough to suggest that data within individual strata approximate normality. The small sample sizes unfortunately preclude testing for lack of fit. It is evident that the rather large variance for stratum 3 (2.15), as compared to the mean of 3.92, was due to a deficient number of samples. However, the variances for the stratified means (0.033 and 0.0053), being at most less than 2.5% of their respective means, clearly demonstrate the applicability of the procedure. As a contrast it is well to note that use of unweighted data from

TABLE 1. Estimation of original population from initial survey data and final population, following the dredge season, from final survey data.

Stratum (h)	Area (*acres*)	n_h	N_h	$\bar{y}_h$	s_h^2
			Initial survey		
1	222.81	4	5703.9	0.44	0.068
2	49.61	6	1270.0	1.17	0.042
3	50.25	3	1286.4	3.92	2.146
4	197.81	5	5063.9	1.80	0.794
			N = 13324.2		
			Final survey		
1	322.67	8	8260.4	0.63	0.083
2	197.81	5	5063.9	0.40	0.046
			N = 13324.3		
			Initial	*Final*	
Mean yield per dredge tow (*bu*)		$\bar{y}_{(st)}$	1.362	0.543	
Variance of estimated mean		$s^2_{(\bar{y}st)}$	0.033	0.0053	
Population estimate (*bu*)		$N\bar{y}_{(st)}$	18,147.56±5703.62	7235.09±2167.12	
Confidence limits (P = .05)			(df = 7)	(df = 10)	

the initial survey results in a calculated sample mean of 1.64 with a variance of 1.80.

POPULATION ESTIMATE FROM CATCH DATA

Detailed catch per unit of effort data collected during the dredge season from the 23 boat fleet was used to provide an independent estimate of the initial population of *M. mercenaria*.

The method, which was first described by Leslie and Davis (1939) and further developed by Ricker (1958), has had wide application in all types of fisheries. The essential feature of their approach is that a plot of catch per unit of effort (C/f) as a function of cumulative catch is negative in slope and linear and the ordinate intercept is an estimator of the original population.

Mean C/f for the dredge fleet of 23 boats was first examined as a function of time (Fig. 2). A surge in C/f during the last week of the dredge season corresponded to a shift of about half the fleet (12 boats) over to the west shore area while sharp dips on the 13th and 24th were due to bad weather.

Dickie (1955) used a procedure for reducing data scatter whereby catch records from a sample fleet are used to extrapolate to the entire fleet. In this study the sample fleet was comprised of six boats having the most consistent catch statistics with respect to the expected values of C/f derived from a linear regression.

The following notation is after Dickie (1955) as modified by Ricker (1958):

Catch of sample fleet	C = 2766.75	80-lb bu
Catch of remainder of fleet	C′ = 8158.26	80-lb bu

The sample fleet regression of C/f on cumulative catch was:

$$\hat{Y} = 10.1882 - 0.001839\,X$$

Therefore, the slope of the regression for the entire fleet was:

$$c = \frac{\bar{c}}{1 + \frac{C'}{C}} = \frac{-0.001839}{3.949} = -0.0004657,$$

giving a regression equation for the entire fleet of:

$$\hat{Y} = 10.1882 - 0.0004657\,X.$$

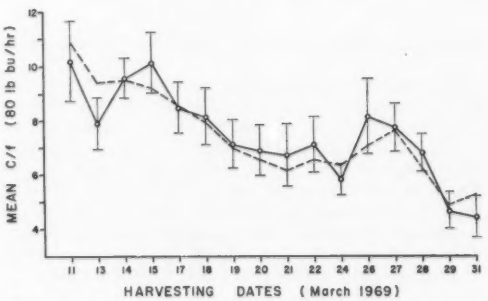

FIG. 2. Mean catches per unit of effort for the entire dredge fleet on successive harvesting days. Bars indicate ± 2 SD. The dashed curve indicates mean C/f for a sample fleet of 6 boats chosen from the entire 23 boat fleet.

Setting $\hat{Y} = O$, the initial population is estimated as:

$$N_O = \frac{10.1882}{0.0004657} = 21{,}880 \text{ 80-lb bu}$$

with confidence limits ($P = 0.05$), calculated from an equation given by DeLury (1951), of 18,170 and 28,510 80-lb bu.

Conclusions

The technique of stratified random sampling allowed the derivation of an estimate of the *M. mercenaria* population which existed prior to a fishing season (18,148 bu) which agrees favorably with a similiar estimate from catch per unit of effort data from the fishing fleet (21,880 bu), despite the fact that it was derived from only 18 dredge samples. Moreover, confidence limits provide an overlap of the two estimates: 12,444–23,852 and 18,170–28,510, respectively, the ranges for the two being similar. The good agreement of these two estimates indicates that the rocking-chair dredge may be expected to provide population estimates well within the range of accuracy required for the management of commercial *M. mercenaria* fisheries. Since the accuracy of estimation is largely dependent upon good evaluation of the dredge efficiency a discussion of factors affecting dredge efficiency is appropriate.

Although Saila et al. (1965) indicated that the rocking-chair dredge apparently integrates small scale cells of contagion, it is concluded from this study that *M. mercenaria* may exhibit large scale aggregations for which dredge data are not normally distributed. Their results give no indication of the existence of such aggregates. While the exact reason for this disparity of results is unknown, it may be postulated that the geometry of the distribution pattern of *M. mercenaria* may be modified in response to mean density of the population or the character and degree of compaction of the substrate or both. Thus, from their data it is estimated that a 10-min dredge tow would yield a mean of about 0.5 bu whereas a mean of 1.36 bu was observed in the initial survey of this study. Moreover, sediments in the area examined by this paper were characterized as being highly compacted with a large sand fraction while the area studied by Saila et al. (1965) has been classified as clayey silt (McMaster 1960) which is significantly less densely compacted at any season of the year (McMaster 1962).

From this discussion certain inferences may be drawn: (1) Since Saila et al. (1965) estimated that their dredge effectively fished 1000 ft^2 during a 3-min tow and one of similiar duration in this study is estimated to fish about 510 ft^2, the efficiency of the dredge is determined by characterisstic of the substrate, principally the degree of compaction. This makes it imperative that dredge efficiency be known for all types of sediment comprising a given study area. (2) While (1) may constitute a disadvantage, nevertheless, the rocking-chair dredge does, to a large extent, smooth the nonrandom distribution of *M. mercenaria* which small scale apparatus, such as grab samplers, do not. Moreover, this property allows population estimation with considerably fewer samples.

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Social Interaction Between Juvenile Coho (*Oncorhynchus kisutch*) and Fall Chinook Salmon (*O. tshawytscha*) in Sixes River, Oregon[1]

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Spawning and emergence of coho and fall chinook salmon overlapped in timing and location in Sixes River, Oregon. In early spring both species were distributed throughout most of the river system. Underwater observations during this period indicated that both species occupied the same habitat. As temperatures increased, coho disappeared from the main river, but continued to occupy cool tributaries. Fall chinook were found primarily in the main river until early summer, when they moved to the estuary.

In flowing-water observation troughs coho assumed social dominance and defended space near the source of incoming food. In allopatry in the troughs, both grew at similar rates, but coho maintained lower population densities than did chinook. In sympatry in the troughs or in cool tributary streams, coho grew faster than chinook. Coho had brighter fin and body colors, greater fin development, deeper bodies, and were heavier than fall chinook of the same length.

Our study suggests that the population of fall chinook salmon in Sixes River might be adversely affected by an increase in numbers of coho. Our evidence suggests that ecology of native fishes should be examined closely before widespread manipulation of fish stocks is encouraged.

STEIN, R. A., P. E. REIMERS, AND J. D. HALL. 1972. Social interaction between juvenile coho (*Oncorhynchus kisutch*) and fall chinook salmon (*O. tshawytscha*) in Sixes River, Oregon. J. Fish. Res. Bd. Canada 29: 1737–1748.

La fraie et l'émergence des saumons coho et chinook d'automne se chevauchent, dans le temps et dans l'espace, dans la rivière Sixes, Orégon. Au début du printemps, les deux espèces sont dispersées par tout le système fluvial. Des observations sous l'eau à cette époque révèlent que les deux espèces occupent le même habitat. A mesure que la température s'élève, les saumons coho quittent la rivière principale, mais continuent d'occuper les tributaires dont la température est plus basse. Les saumons chinook d'automne séjournent surtout dans le cours d'eau principal jusqu'au début de l'été, pour ensuite émigrer vers l'estuaire.

Dans des bassins d'observation à flot continu, les saumons coho acquièrent une dominance sociale et défendent un territoire à proximité de la source de nourriture. Dans des conditions allopatriques en bassins, les deux espèces croissent à un même rythme, mais les saumons coho maintiennent une densité de population plus faible que les saumons chinook. Dans des conditions sympatriques en bassins ou dans les tributaires plus frais, les saumons

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coho croissent plus rapidement que les saumons chinook. Les saumons coho ont une coloration plus brillante sur les nageoires et le corps, des nageoires plus développées, un corps plus haut et un poids plus grand que les saumons chinook d'automne de même longueur.

Les résultats de cette étude nous portent à croire que l'augmentation du nombre de saumons coho pourrait avoir des effets adverses sur la population de saumons chinook d'automne de la rivière Sixes. On devrait donc étudier de près l'écologie des poissons indigènes avant de pousser trop avant la manipulation des stocks.

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Coho salmon (*Oncorhynchus kisutch*) and fall chinook salmon (*O. tshawytscha*) occur together in many of the coastal streams of western North America. In Sixes River, on the south coast of Oregon, the timing and location of spawning of these two species overlap; consequently, juveniles are found together. Coho and fall chinook salmon may interact because their ecological requirements are similar. Earlier studies of each species have suggested that territoriality and agonistic behavior may function in the regulation of population numbers relative to available food and space (Chapman 1962, 1966; Reimers 1968). Thus, our study was designed to examine the interaction between juvenile coho and fall chinook salmon. Specific objectives were: (1) to examine habitat preferences and interaction of coho and fall chinook in Sixes River, and (2) to determine the outcome of any social interaction in terms of residence and growth. The main portion of this investigation was conducted during the spring and summer of 1970.

Interaction between juvenile salmonids has been examined in some detail. Recently Lister and Genoe (1970) suggested that size-related differences in habitat selection might minimize interaction between underyearling coho and fall chinook in the Big Qualicum River, British Columbia. They found that chinook emerged first, grew at a faster rate, and subsequently moved into water of progressively higher velocity before coho. Differences in habitat selection reduced behavioral interaction. These differences persisted until the downstream migration of chinook, 2 to 3 months after emergence. Other studies have also shown that young salmonids segregate in nature (Hartman 1965; Nilsson 1967; Everest and Chapman 1972).

Materials and Methods

The Study Area

Sixes River is a short coastal drainage located 8 km north of Port Orford, Oregon, and drains an area of approximately 340 km^2. Most of the watershed, once extensively logged, now consists of second-growth Douglas fir combined with mixed broad-leaved species. Most tributaries remain below 20 C throughout the summer, whereas temperatures in the main river commonly exceed 25 C. Approximately 2500 adult salmon spawn in this system each year, of which about 90% are fall chinook and 10% are coho. Cutthroat trout (*Salmo clarki*) and steelhead trout (*Salmo gairdneri*) are also present in the Sixes system.

Studies were concentrated on Crystal Creek, a tributary of Sixes River 6 km inland from the mouth, which drains about 24 km^2. The densely shaded upper section has cool temperatures in summer, but temperatures in the exposed lower valley often exceed 20 C. Coho are estimated to comprise about one-third of the total number of spawning salmon.

Natural Populations

To determine spatial distributions and patterns of growth, juvenile salmon were seined from the main river and selected tributaries at 3-week intervals from March to June 1970. Fish were anesthetized with M.S. 222, measured to 1-mm fork length, and returned to the stream. To insure representative catches in the various habitats sampled, several types and sizes of seines were used for capturing fish.

To examine the microhabitat distribution of juvenile coho and chinook in the stream, we conducted underwater surveys by snorkeling. These observations were made periodically during spring and summer.

Experimental Populations

Studies of experimental populations were conducted in observation troughs described by Reimers (1970). Each trough was divided into a riffle and a pool. Observations of fish activity were made through plexiglass windows. Water from a natural stream flowed over the riffle, through the pool, and downstream into a trap at a rate of about 110 liters/min. During the experiments, water temperatures ranged from 9 to 12 C. The experimental procedure involved stocking the troughs with different sizes and proportions of coho and chinook. Volitional residence was allowed in all but one final experiment in the spring of 1972. This experiment was conducted so that downstream migration was prevented and the initial stocking ratios and densities were maintained. In the experiments with volitional residence, deviations from the initial stocking ratio could occur through differential out-migration.

For each experiment, individual fish seined from tributaries of Sixes River were weighed to 1 mg, measured to 0.5-mm fork length, and placed into the troughs. Fish that moved downstream into the traps during the

first 2 days of each experiment were returned to the troughs. Subsequently, numbers of each species of fish in the riffle, pool, and trap were usually recorded daily; fish in the trap were discarded. Behavioral observations totaling about 30 hr were made during these periods. When downstream movement had ceased for at least 5 days, experiments involving volitional residence were terminated and individual fish were weighed and measured.

Instantaneous rates of growth in weight per day (Ricker 1958) were estimated for fish that remained in the troughs until termination of the experiment. Fish were not individually marked; the initial size of each was estimated as the mean weight of all fish originally planted. Weight gain of individual fish was estimated by subtracting final weight from the average initial size. This procedure probably resulted in an overestimation of individual growth rates for both species because the smaller fish left early in the experiment. However, our comparisons are based on relative differences between coho and chinook, and the ranges of initial sizes of the two species were selected to be as similar as possible.

In the first experiment we planted eyed eggs of coho and chinook in the gravel of the observation troughs. Eggs were taken from sexually mature fish from the Sixes and adjacent Elk rivers and incubated at Elk River Salmon Hatchery. Since the period of embryonic development is longer for chinook, they were spawned before coho. This procedure permitted fry of both species to emerge at nearly the same time. Volitional residence was allowed, but downstream migrants were not returned to the troughs.

Color Patterns and Morphology

Coloration and morphology were described from fish observed in the laboratory, the troughs, and the stream. Fish taken to the laboratory were anesthetized in M.S. 222 to relax their chromatophores, and then examined with a binocular microscope.

Measurements of fin and body morphology were made with vernier calipers on preserved specimens from Sixes River. Measurements included fork length, body depth, length of the leading edge of the dorsal and anal fins (height of the fins), and length of the pelvic fins (Hubbs and Lagler 1958). Fork length was recorded to the nearest 1 mm; all other measurements were recorded to the nearest 0.1 mm.

Length–weight relations for the two species were calculated from fish captured in the tributaries of Sixes River. Immediately after capture, they were transported live to the laboratory, anesthetized in M.S. 222, measured to 0.5-mm fork length, and weighed to 1 mg.

Results

Distribution

Spawning of coho and fall chinook salmon in Sixes River overlapped in both timing and location. Coho were usually found in the upper areas. Chinook spawned in the upper main river and in lower sections of the tributaries. Timing of emergence was similar for the two species, although peak emergence of coho occurred about 2 weeks prior to peak emergence of chinook (Table 1).

As a result of similarity in both spawning time and location, newly emerged coho and chinook were found together during April and May (Fig. 1). Fry of both species occurred in the spawning tributaries and in the main river, but coho were more numerous in the tributaries and chinook were more abundant in the main river. As temperatures increased in late spring and early summer (Fig. 2), coho were no longer found in the main river (Fig. 1). However, they were still abundant in the cool tributary streams. Chinook were present in the main river as well as the tributary streams.

Comparison of the numbers of juvenile coho residing in Hays and Crafton creeks suggests the effect of temperature in influencing distribution of this species. Most of the watershed of Crafton Creek has been logged and part of the lower section recently sprayed with a defoliant. As a result, the stream has little shade and is considerably warmer than Hays Creek (Fig. 2). Although spawning and emergence of coho occurred in Crafton Creek, no juveniles were present after May. In contrast, coho that emerged in Hays Creek remained throughout the summer (Fig. 1).

Approximately 20 hr of snorkeling observations during April and May 1971 indicated that recently emerged coho and chinook shared a common habitat. Both species were observed in close association in backwater eddies near shore. They were distributed throughout the water column and were actively feeding on drift. From these preliminary observations, coho and chinook appeared to be utilizing

Table 1. Estimated times of spawning and emergence of coho and fall chinook salmon in Sixes River. Estimates are based on counts of spawning fish, observations of first fry emergence, and embryonic development at an average water temperature of 8 C.

Spawning period		Emergence period	
Peak	Range	Peak	Range
Coho			
Late Dec.	Mid-Nov. to late Jan.	Early Apr.	Early Mar. to mid-May
Chinook			
Early Dec.	Mid-Nov. to late Jan.	Late Apr.	Mid-Mar. to early June

only margins of the stream in early spring. During the summers of 1970 and 1971 individuals of both species were found together in pools near the downstream end of riffles, actively feeding throughout the water column.

Growth

At emergence, fall chinook in our experimental systems were about 35% heavier than coho (0.47 vs. 0.35 g). In Crystal Creek coho were larger than chinook soon after emergence. From May 10 to August 25 the average weight of coho was greater than that of chinook in 19 out of 20 samples. McGie and Lenarz (MS 1964) also found that coho were larger than chinook in Crystal Creek following a period of stream rearing.

We thought that the apparent reversal in relative size might be the outcome of differential rates of growth caused by social interaction. To test this hypothesis, coho and chinook of similar sizes were combined in observation troughs (Table 2).

In the two experiments where both species were in allopatry, some chinook grew at the same rate as the fastest growing coho. Whether combined with chinook or not, coho always grew rapidly (Fig. 3). However, when chinook were combined with coho, they grew more slowly than when alone.

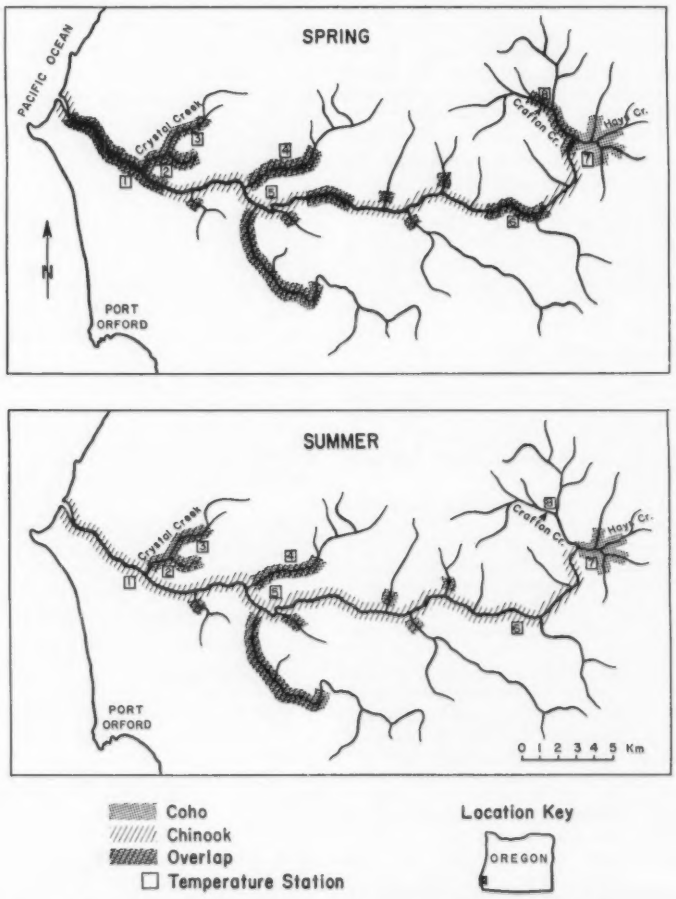

FIG. 1. Distribution of juvenile coho (*Oncorhynchus kisutch*) and fall chinook salmon (*O. tshawytscha*) in Sixes River in spring and summer, based on seining (Fish Commission of Oregon, 1964–70 unpublished data).

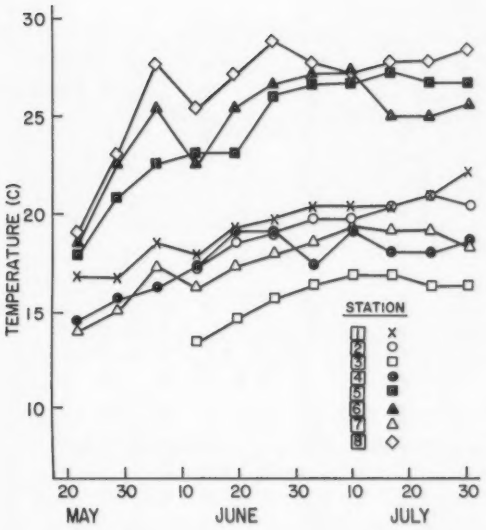

FIG. 2. Maximum weekly temperatures in Sixes River and selected tributaries during the summer of 1970. Data on stream temperature were gathered with thermographs and maximum–minimum thermometers placed throughout the river system (Fig. 1).

AGONISTIC BEHAVIOR

Intraspecific agonistic behavior, as described for coho (Chapman 1962) and fall chinook (Reimers 1968), was observed in the troughs during these experiments. Interspecific agonistic behavior included nipping, chasing, lateral display, submission, and fleeing. During each experiment the rate of agonistic behavior progressively decreased to a low level.

Hierarchies were formed in both sympatric and allopatric groups leading to differential out-migration and unbalanced species distribution in the troughs (Fig. 3). In every experiment where coho were combined with chinook, coho defended positions at the upstream end of the riffle, where drifting food organisms were first available to fish (Fig. 4). This occupation of prime feeding areas led to better growth by coho than chinook regardless of the stocking density, species ratio, or relative size of individuals. Even with unnaturally high densities of fish imposed in our final experiment, a few coho defended upstream areas and tended to exclude chinook from that area through social behavior (Table 3). In allopatry, chinook were almost evenly distributed between the riffle and the pool (Fig. 4).

In the troughs, chinook tolerated a larger number of individual fish per unit area than did coho. In allopatric groups, a larger number of chinook than coho remained in the troughs until termination of an experiment. When they were combined with coho, few chinook remained until termination. Chinook did not appear to influence the numbers of coho remaining in the troughs. Whether combined with chinook or not, rather small numbers of coho remained (Table 2).

In Crystal Creek, interaction between coho and chinook, including lateral display, nipping, and chasing, was observed during underwater surveys in early spring. In summer, intraspecific interaction was evident in both species, but little interaction between species was observed, even though they were commonly observed in close proximity to one another.

COLOR PATTERNS AND MORPHOLOGY

Color patterns of coho and fall chinook in Sixes River differed considerably. Juvenile coho were yellow-brown with dark brown backs. Their parr marks were narrow and dark brown but did not contrast sharply with the rest of their body. All fins were bright orange. Chinook were silvery or light yellow with blue-green or brown backs. Parr marks were wide and black, and contrasted sharply with the rest of the body. Their fins were yellow and less conspicuous than those of the coho. Major differences between the two species were found in the dorsal, anal, and pelvic fins, but the caudal and pectoral fins differed only in general coloration as described above.

Size-related seasonal differences in general coloration were noted. Both newly emerged and large chinook were more silvery than fish of intermediate size. General coloration of both species became less vivid near the end of summer.

The height of the dorsal fin was distinctly greater for coho than chinook (Fig. 5A) and variation was greater for coho. The height of the anal fin was much greater for coho than chinook (Fig. 5B) and variation was again greater for coho.

At emergence, the leading edge of the dorsal fin of coho was black proximally and white distally (Fig. 6). Subsequently, the black pigment appeared to extend distally behind the white band, which had extended proximally to the base of the fin. Development of vivid coloration required approximately 2 weeks from emergence. By then the leading edge of the dorsal fin was white, backed by a black band; the remainder of the fin was orange.

At emergence, the dorsal fin of chinook contained only a few scattered chromatophores and was

TABLE 2. Number and mean size of fish at the outset and termination of experiments conducted in the observation troughs during spring 1970. Volitional residence was provided. In experiments I and II the sympatric groups were replicated in separate troughs. For experiments III–V only two troughs were available. Length is shown in centimeters and weight in grams.

	Allopatric groups							Sympatric groups						
		Start			Finish				Start			Finish		
Expt	Species	No.	Mean length (*range*)	Mean weight (*range*)	No.	Mean length (*range*)	Mean weight (*range*)	Species	No.	Mean length (*range*)	Mean weight (*range*)	No.	Mean length (*range*)	Mean weight (*range*)
I	Coho	600	Eyed eggs	0.35 (0.34–0.36)	3	4.55 (4.30–4.80)	0.91 (0.73–1.09)	Coho	300	Eyed eggs	0.35 (0.34–0.36)	2	4.60 (4.30–4.90)	0.92 (0.73–1.13)
								Chinook	300	Eyed eggs	0.47 (0.46–0.48)	12	4.16 (4.05–4.80)	0.65 (0.52–1.00)
	Chinook	600	Eyed eggs	0.47 (0.46–0.48)	16	4.28 (4.00–4.90)	0.70 (0.50–1.09)	Coho	300	Eyed eggs	0.35 (0.34–0.36)	2	4.75 (4.60–4.90)	1.00 (0.88–1.12)
								Chinook	300	Eyed eggs	0.47 (0.46–0.48)	10	4.16 (4.10–4.30)	0.60 (0.56–0.66)
II	Coho	41	4.36 (4.00–4.50)	0.78 (0.58–0.85)	1[a]	5.10	1.46	Coho	20	4.26 (4.00–4.40)	0.71 (0.58–0.79)	3	5.10 (4.70–5.60)	1.48 (1.09–1.96)
								Chinook	20	4.26 (4.00–4.40)	0.65 (0.52–0.73)	3	4.57 (4.45–4.70)	0.92 (0.85–1.00)
	Chinook	42	4.40 (4.00–4.50)	0.72 (0.52–0.79)	7	4.77 (4.10–5.60)	1.06 (0.59–1.89)	Coho	20	4.26 (4.00–4.40)	0.71 (0.58–0.79)	2	5.62 (5.45–5.80)	1.92 (1.67–2.16)
								Chinook	20	4.26 (4.00–4.40)	0.65 (0.52–0.73)	1	4.45	0.72
III	Chinook	18	4.10 (3.90–4.35)	0.58 (0.45–0.80)	6	4.48 (4.20–5.10)	0.89 (0.68–1.37)	Coho	5	4.08 (3.80–4.30)	0.61 (0.48–0.69)	3	4.97 (4.80–5.05)	1.22 (1.10–1.35)
								Chinook	12	4.13 (3.90–4.40)	0.60 (0.45–0.75)	0		
IV	Chinook	44	4.22 (3.90–4.00)	0.70 (0.43–0.84)	9	4.54 (4.10–5.45)	0.89 (0.47–1.67)	Coho	22	4.21 (3.90–4.50)	0.71 (0.42–0.88)	4	5.05 (4.30–5.95)	1.42 (0.82–2.26)
								Chinook	22	4.34 (3.80–4.60)	0.71 (0.41–0.89)	1	4.30	0.67
V	Chinook	12	4.09 (4.00–4.20)	0.59 (0.52–0.61)	8	4.52 (4.00–4.90)	0.89 (0.66–1.19)	Coho	4	4.05 (4.00–4.10)	0.60 (0.58–0.63)	4	4.62 (4.40–4.80)	1.00 (0.77–1.12)
								Chinook	8	4.10 (4.00–4.20)	0.56 (0.52–0.61)	4	4.32 (4.10–4.70)	0.70 (0.54–1.07)

[a]Near the termination of the experiment, three coho moved downstream following a temporary cessation of flow.

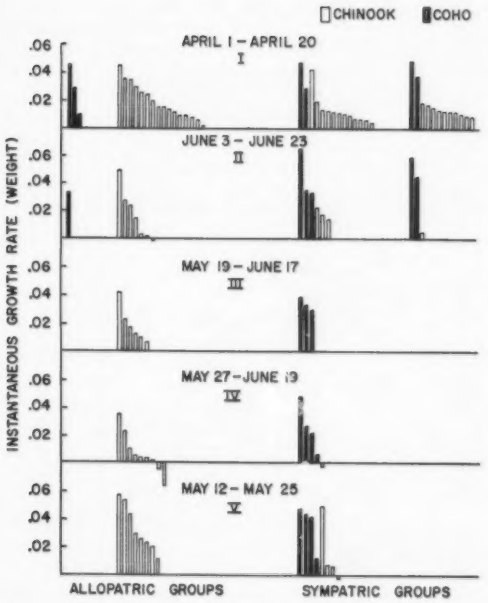

FIG. 3. Estimated instantaneous growth rate (per day) for underyearling coho (*Oncorhynchus kisutch*) and fall chinook salmon (*O. tshawytscha*) during spring 1970 in the observation troughs, where volitional residence was provided. Each vertical bar represents one fish that remained in the trough until termination of the experiment. Experiments I–V are in order of increasing initial advantage to chinook based on size and numbers. In Experiment I, coho began emerging 7 days before chinook, an emergence pattern similar to that found in the stream environment. See Table 2 for initial conditions.

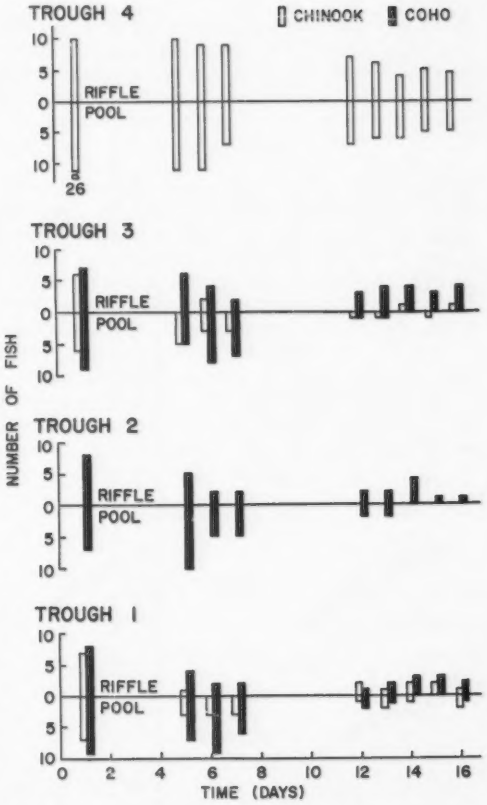

FIG. 4. Relation between the numbers of underyearling coho (*Oncorhynchus kisutch*) and fall chinook salmon (*O. tshawytscha*) present in the riffle and pool in the observation troughs during the period June 3–19, 1970 (Experiment II). Decline in numbers of fish with time resulted from downstream movement.

nearly transparent (Fig. 6). Subsequently, a proximal band of black developed simultaneously with the white and orange distally. As in coho, full development of coloration took about 2 weeks. At that time, the leading edge of the dorsal fin of chinook was white distally, but black proximally in contrast to coho. Chinook also differed from coho in possessing an orange band behind the white leading edge of the dorsal fin. The remainder of the fin was yellow.

Color patterns of the anal fins were similar to those of the dorsal fins (Fig. 6). At emergence, coho already had a band of black pigmentation behind the white leading edge of the fin. Both bands became more prominent in older fish. The remainder of the fin was orange.

At emergence, the white leading edge of the anal fin of chinook was only faintly visible but developed rapidly during the first week of stream residence. The entire leading edge of the anal fin was white. An orange band developed directly behind the white leading edge and graded into pale yellow over the remainder of the fin.

Pelvic fins of coho were only slightly longer than those of chinook. However, color patterns of the fins were quite dissimilar. Pelvic fins of coho were completely orange, but those of chinook had a distinct white leading edge backed by an orange band that graded into pale yellow over the remainder of the fin.

Coho were heavier than chinook over the entire range of lengths examined (3.5–7.5 cm). Regressions of the natural logarithm of weight on the logarithm

TABLE 3. Distribution of coho and fall chinook salmon confined in observation troughs without volitional residence, March 28–April 17, 1972. Because of higher average densities in this experiment and the resultant decrease in food availability, distribution on the riffle was subdivided into upper (where food entered) and lower halves. Values shown are results of counts taken on 10 days during the experiment. Movement of fish during the counting period resulted in minor discrepancies in daily totals.

Trough no.	Species (No. stocked)	Coho						Chinook					
		Upper riffle		Lower riffle		Pool		Upper riffle		Lower riffle		Pool	
		Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range
1	Coho (22)	1.0	–	4.3	2–5	13.1	11–15						
2	Chinook (22)							4.5	3–6	5.4	3–7	10.3	6–14
3	Coho (11), chinook (11)	1.7	1–3	3.5	2–5	5.0	3–8	0.2	0–2	4.0	3–6	5.3	2–7
4	Coho (11), chinook (11)	1.3	1–3	3.6	1–7	5.0	2–8	0.0	–	3.0	1–6	7.2	5–10

of length computed for each species yielded the following relations:

$$\text{coho } W = 0.00506\ L^{3.41}$$

$$\text{chinook } W = 0.00378\ L^{3.55}$$

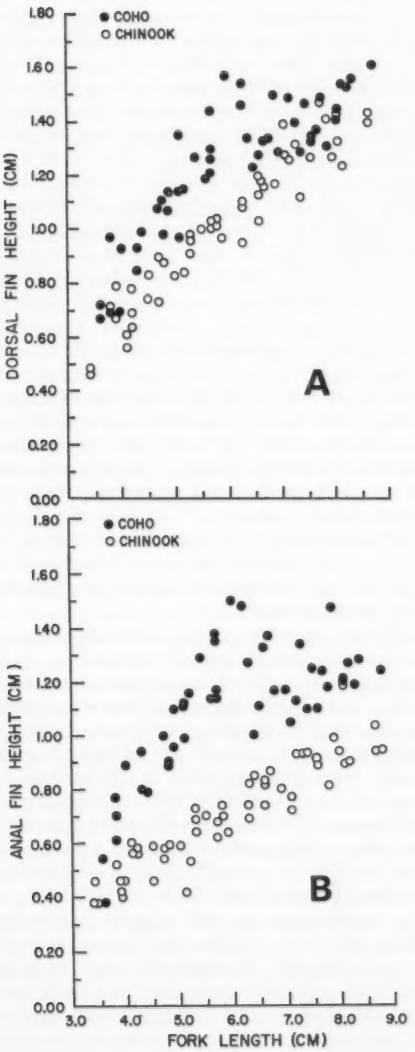

FIG. 5. Juvenile coho (*Oncorhynchus kisutch*) and fall chinook salmon (*O. tshawytscha*) in Sixes River: A) relation between height of dorsal fin and fork length, B) relation between height of anal fin and fork length.

In another sample of fish (3.5–9.0 cm), coho had deeper bodies than chinook over the entire length range. The differences in both weight and body depth were shown statistically significant ($P < .05$) by analysis of covariance.

Discussion

Chronological and spatial overlap in freshwater residence resulted in social interaction between juvenile coho and fall chinook salmon in Sixes River. Because both species are dependent upon a period of extended freshwater residence (Chapman 1962; Reimers MS 1971), interspecific interaction may ultimately influence survival, through distribution and growth of juveniles.

When together in cool tributary streams and observation troughs, coho grew faster than chinook. When alone in troughs individuals of both species grew at similar rates. Coho did not seem to be

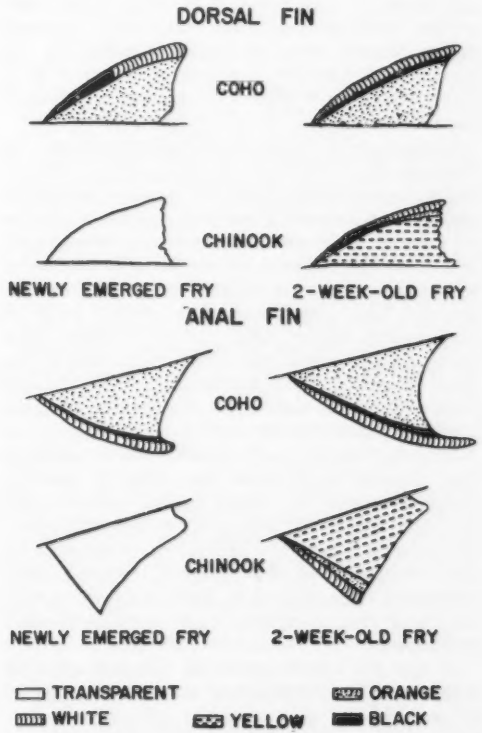

FIG. 6. Diagrammatic sketches of the dorsal and anal fins of recently emerged and 2-week-old coho (*Oncorhynchus kisutch*) and fall chinook salmon (*O. tshawytscha*) in Sixes River.

influenced by the presence of chinook. However, chinook appeared to be severely affected by coho, as both their rate of growth and their ability to maintain position in the troughs were reduced. Since residence and growth in fresh water are required for production of returning adults, chinook must be successful in areas other than cool tributary streams occupied by coho. Recent studies have shown that most of the returning chinook spend about 3 months in the main river and 3 months in the estuary before entering the ocean in autumn (Reimers MS 1971).

In Sixes River, coho and chinook emerged at similar times, utilized similar habitats, and interacted. Owing to nearly complete overlap in timing of emergence, microhabitat segregation based on a size difference did not occur. Both species shared a common habitat in spring. However, distributions of these two species changed as temperatures increased in the main river. We speculate that, as temperature increases, coho leave the main river and move into the cooler tributaries or die. Only a few underyearling coho have been captured during several years of extensive seining in the estuary and fyke-net sampling of the river as it enters the estuary (Fish Commission of Oregon unpublished data).

From studies of coho and fall chinook in the Big Qualicum River, British Columbia, Lister and Genoe (1970) suggested that differences in time of emergence and growth rate of these two species allow for coexistence. From their seining data, they suggested that coho and chinook did not interact because of size-related differences in habitat selection. Chinook emerged first, grew faster, and selected areas of progressively higher water velocity before coho reached a size where they could utilize such areas. They suggested that segregation results simply from difference in size. Coho and chinook of equal length preferred similar habitat.

Although Lister and Genoe (1970) reported that chinook grew faster than coho in the Big Qualicum River, we found similar growth rates for both species in allopatric groups. However, they assumed that the progressive differences in size between coho and chinook resulted from differential rates of growth. As they noted, recruitment and emigration may have complicated their comparisons.

In the Big Qualicum River, chinook emerged before coho and maintained a size advantage in an environment that permitted microhabitat segregation. Because of overlap in emergence, microhabitat segregation did not occur in Sixes River. However, differential response by the two species to an increase in stream temperature may have contributed to segregation between tributaries and main stem following the emergence period.

Fall chinook appear to possess a greater potential for growth at high temperatures than do coho. When each species was held in groups of 10 in 50-liter aquaria and fed to excess, coho grew slightly faster (55 mg/g/day) than fall chinook (51 mg/g/day) at 13 C. However, at 18 C fall chinook grew much faster (62 mg/g/day) than coho (35 mg/g/day) (T. O. Thatcher, Department of Fisheries and Wildlife, Oregon State University unpublished data). Although food is not unlimited in the natural environment, these temperature-related differences in growth rate may, in part, explain the distribution of these two species in Sixes River.

In addition to these temperature-related physiological differences, sympatric populations of coho and chinook may have evolved distinct behavioral adaptations related to their pattern of stream life. In the observation troughs, coho were more aggressive than chinook and tolerated fewer individuals of their own species than did chinook. The extensive development of agonistic behavior in the coho may be related to its length of stream residence. The coho must adjust its population to levels compatible with low streamflow in late summer, a period when space and, presumably, food are much reduced compared to spring. Because most chinook reside only 3 months in fresh water, the population may have evolved a pattern of behavior that involves small territory size. The majority of chinook have moved to the estuary or ocean before low flow in late summer restricts the availability of food and space in the stream.

Coho and chinook in Sixes River appear to have also evolved morphological adaptations to the freshwater mode of life that are consistent with their length of residence. Coho in Sixes River had brighter colors, greater fin development, deeper bodies, and were heavier than chinook of the same length. In Alaska, most chinook spend a full year in fresh water (Meehan and Siniff 1962). Coloration and fin development of these chinook are sufficiently extensive that distinguishing between coho and chinook is difficult without the use of additional characters (Meehan and Vania 1961).

The involvement of color patterns and fin morphology in social behavior has been suggested for another salmonid (Keenleyside and Yamamoto 1962). Although our data were not sufficient to determine whether color differences were important in social dominance, we believe this aspect is sufficiently interesting to warrant further investigation. Likewise, the behavioral and physiological responses of the two species to temperature increase seems to be another fruitful area for further research.

Because of various physiological, behavioral, and morphological characteristics of the populations we studied, coho appear to be adapted to long-term residence in cool, small streams. Chinook, on the other hand, appear to be adapted to rearing conditions in the main river and estuary. Consequently, mutual agonistic behavior in the Sixes system may favor coho in cool tributaries and chinook in the main river and estuary. These ideas seem consistent with those of Nilsson (1965), who suggested that intense interspecific competition in sympatric populations of similar or closely related species forces each species to compete at its "ecological optimum", or under those conditions to which it is best adapted. In this way interspecific interaction may promote segregation in Sixes River. Even though segregation in Sixes River may not be the direct result of territorial conflict, interspecific agonistic behavior may play an important role in the distribution of juvenile coho and fall chinook salmon.

This study did not include the two species of trout present in the Sixes system. Their presence could influence the interaction between coho and chinook. However, limited underwater observations during spring and summer suggest that mechanisms of segregation, similar to those reported by Everest and Chapman (1972) for steelhead trout and chinook salmon, are in evidence. These mechanisms appear to minimize the interaction between salmon and trout in Sixes River.

The extent to which our observations on coho–chinook interaction are relevant only to the Sixes River watershed must be considered. Recent agricultural and lumbering activity in the watershed appears to have considerably altered the habitat, especially stream temperature. The extent to which watershed manipulation has altered the historic relation between these two species is unknown. However, response of both species to recent changes in stream temperature may have played an important role in modifying interspecific interaction. Further research should be directed to both long- and short-term effects of land management practices on interaction of these and other fish species.

Our results suggest that the ecology of native populations should be examined closely before manipulation of fish stocks is encouraged in any river system. Widespread stocking of fish from hatcheries is becoming more common. This management practice may lead to short-term increases in population levels, but could result in undesirable long-term consequences. For example, if large numbers of hatchery coho were stocked in Sixes River, increased interaction might result in the replacement of chinook by coho in the main river during spring. The coho, however, would presumably not be successful in the main river as temperatures increased. The net result could be a decrease in total salmonid production from the Sixes system. Selection among alternative strategies for stock enhancement, including traditional hatchery means, should be based upon sound biological justification.

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Summer Storage of Energy and Its Use for Winter Metabolism and Gonad Maturation in American Plaice (*Hippoglossoides platessoides*)[1,2]

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MacKinnon, J. C. 1972. Summer storage of energy and its use for winter metabolism and gonad maturation in American plaice (*Hippoglossoides platessoides*). J. Fish. Res. Bd. Canada 29: 1749–1759.

American plaice (*Hippoglossoides platessoides*) in St. Margaret's Bay, Nova Scotia, had an annual energy storage cycle in which a mature 35 cm female stored 92 kcal during the summer period and used this energy for metabolism (72 kcal) and gonad maturation (20 kcal) in winter months. An additional 21 kcal was stored in the ovary during the summer period. These energy changes occurred in a fish with a total energy content of approximately 300 kcal and an annual energy increment of 51 kcal due to growth in length. The annual energy variation in immature females and males was less than in mature females. A comparison of summer production (143 kcal, excluding gonad energy) with net annual production (51 kcal) for a 35 cm female plaice indicated that higher yields would be obtained by harvesting at the end of the summer period than by taking the same fish at the end of the overwintering period.

MacKinnon, J. C. 1972. Summer storage of energy and its use for winter metabolism and gonad maturation in American plaice (*Hippoglossoides platessoides*). J. Fish. Res. Bd. Canada 29: 1749–1759.

Le cycle annuel de stockage d'énergie de la plie canadienne (*Hippoglossoides platessoides*) de la baie St. Margaret, Nouvelle-Ecosse, permet à une femelle mûre de 35 cm de longueur d'emmagasiner 92 kcal durant les mois d'été et d'utiliser cette énergie pour le métabolisme (72 kcal) et la maturation des gonades (20 kcal) durant les mois d'hiver. Un supplément de 21 kcal est emmagasiné dans l'ovaire durant les mois d'été. Ces variations d'énergie ont été observées chez un poisson dont le contenu énergétique total était d'environ 300 kcal, avec augmentation annuelle de 51 kcal due à la croissance en longueur. Les variations annuelles de l'énergie des femelles et des mâles immatures sont moindres que celles des femelles sexuellement mûres.

Une comparaison de la production estivale (143 kcal, excluant l'énergie orientée vers les gonades) avec la production annuelle nette (51 kcal) chez une femelle de 35 cm de longueur nous donne une idée des rendements accrus qu'on obtiendrait si on récoltait ces plies à la fin de l'été plutôt qu'à la fin de la période d'hivernage.

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During summer American plaice (*Hippoglossoides platessoides*) not only feed and grow but also store energy which is used for metabolism and gonad maturation in winter and early spring, when feeding and growth virtually cease. Energy content of an individual fish therefore increases each year, accompanied by a seasonal cycle. This paper documents the cycle observed in plaice of St. Margaret's Bay, Nova Scotia, and considers the adaptive significance of this phenomenon as compared to an alternative involving year-round feeding.

Previous investigations on seasonal changes in condition (LeCren 1951; Bagenal 1957) and chemical composition (Love 1970) have provided indirect evidence for annual energy storage cycles in fish but there have been few direct observations (Sandercock MS 1969; Mann et al. 1972) based upon energetics data. An association of the cycle with the migration–

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overwintering–spawning–feeding sequence is expected (Nikolsky 1963) and it is often assumed, tacitly or explicitly, that temperature is the primary controlling factor. In St. Margaret's Bay, however, the temperature of water inhabited by plaice is 3 ± 3 C during the year (Sharaf-el-Din et al. 1971) so that an alternative explanation to an energy storage cycle correlated with temperature is required.

Materials and Methods

American plaice were taken by otter trawl in St. Margaret's Bay, N.S., on nine occasions between March, 1970, and February, 1971. During this period about 800 fish were examined, 950 samples of body and gonad materials were dried, and calorific determinations were made on 260 of these samples.

Fish were randomly selected from each catch and sorted into samples defined by three categories: (1) mature females, 30–40 cm; (2) immature females, 30–40 cm; and (3) mature and immature males, 20–30 cm. The length ranges were chosen to provide data for fish of "standard" lengths corresponding to the midlengths of the sample categories. These standard lengths of 35 cm and 25 cm for females and males, respectively, are approximately equal to the length at median age of plaice in the bay population.

Approximately 30 fish were selected for each sample category, in accord with the criterion that the weight at midlength of the sample should be determined, with 95% confidence, within ± 3%. The weight at midlength was computed from a power curve regression of gutted weight on length for fish in each sample category and confidence limits were evaluated from the log-transformed data (Sokal and Rohlf 1969).

Samples of material from at least 15 specimens in each category for each collection date were selected for drying and 3–6 subsamples of the dried material were randomly chosen for calorimetry. These sample sizes were based upon the criterion that mean values for percentage dry material and energy per unit dry weight should be determined, with 95% confidence, within ± 3% and ± 6%, respectively.

Sampling took place at about 4 week intervals from March until July and at 6 week intervals during the rest of the year. These times were chosen so that relatively more effort was devoted to sampling during the period when major changes in energy storage were expected.

Following selection from the trawl catch, the fish were packed on ice and transported to the lab where measurements were made and samples were taken for drying. Overall length from snout to tip of mid caudal ray was measured to 0.1 cm. Gross body weights were determined to within 0.1 g. Gonads and viscera were removed and gutted weight recorded. Gonad weights were measured to 0.01 g and state of development (Pitt 1966) was assigned. Viscera samples were prepared by removing stomach and intestinal contents and blotting on paper. Body samples were taken by cutting a section across the fish behind the visceral cavity.

Samples of body and gonads of fish in all sample categories were taken routinely. Viscera samples were taken on only two occasions during the year, spring and autumn. Samples of heads from males and females were obtained once.

All sample materials were oven dried at 60 C for 4–5 days. Preliminary tests were carried out to determine adequate drying times to constant weight. As a check on the dry/wet weight ratios determined by drying at this temperature, equivalent samples were freeze-dried and the results compared with those for oven drying. Ovaries of mature females were divided ,and one half was freeze-dried and the other oven-dried at 60 C for 5 days. The dry/wet weight ratio for freeze drying was 0.272 ± 0.006 versus 0.267 ± 0.006 for oven drying.

Whole gonad and viscera samples were dried whereas body sections constituting about 15% of gutted weight were assumed to be representative of body materials. On one occasion 14 body sections and 13 whole bodies less head were dried. The dry/wet weight ratio for body sections was 0.185 ± 0.006 versus 0.186 ± 0.006 for whole bodies.

After drying, the materials were weighed and then ground into a fine powder with a Krups coffee grinder. The samples were placed in separate vials and stored in a desiccator.

A Phillipson (Phillipson 1964) micro-bomb calorimeter was used for determination of energy content of all materials.

The calorific value of freeze-dried materials was compared with that of oven-dried materials and no significant difference was found. When the two methods of drying mature ovaries were compared, samples of the materials were analyzed for energy content. The freeze dried materials contained 5387 ± 306 cal/g while the oven dried materials had 5288 ± 136 cal/g.

Energy content of body sections was not found to differ significantly from that of whole body material. At the time the dry/wet weight ratios of these materials were compared samples were analyzed for calorific value; energy content of body sections was 4734 ± 297 cal/g versus 4500 ± 90 cal/g for whole bodies.

Seasonal Cycle Observations

Annual energy storage patterns were derived from data obtained for seasonal variation in wet weight, percent dry weight, and energy per unit dry weight of body and gonad components.

Body weight — The seasonal variation in body weight of standard length fish for each sample category is indicated by the data presented in Table 1. Exponents of the regressions used in computing these numbers varied from 2.6 to 3.3 but did not differ significantly ($P < 0.05$) from 3.0; the intercepts did not exhibit any regular pattern of variation with season or difference between sexes.

For all three sample categories the general trend of gutted weight at standard length versus time indicates a minimum weight and condition in April and a maximum in September. The variation in weight at standard length was largest and most regular in mature females. Weights of fish captured in November were somewhat lower than the general trend would suggest; percent dry weight and energy per unit dry weight of these materials were also lower than suggested by overall trends. In general, the times of minimum and maximum condition coincided with corresponding extreme values of percent dry weight and energy per unit dry weight of body materials.

Gonad weight — The ovary weight of a 35 cm mature female varied from 1.6% of body weight after spawning to about 10% of body weight prior to spawning whereas the ovaries of immature fish of similar length weighed close to 0.8% of body weight throughout the year. The ovary weights increased consistently throughout the cycle (Table 1). The data on ovary weights of immature females provide little evidence for a seasonal cycle, the variations appearing to be more closely related to changes in overall body condition than to the reproduction cycle.

Testes weight of 25 cm males (Table 1) varied from 1 to 2% of body weight during the year, with a maximum in February–March prior to spawning and a minimum from June to September. As immature and spent testes were not distinguished from mature testes, the computed weights decreased as spent fish became relatively more frequent in the sample. Also, the testes weights of mature males of this length would be slightly larger than the

TABLE 1. Body and gonad weights (g) of American plaice from St. Margaret's Bay, 1970–71. Values computed for fish of midlengths in samples of 30–40-cm females (numbers examined in brackets) and 20–30-cm males.[a]

	Mature females (*35 cm*)		Immature females (*35 cm*)		Mature and immature males (*25 cm*)	
Month	Body wt	Ovary wt[b]	Body wt	Ovary wt	Body wt	Testes wt
Mar.	281.7	16.9	284.8	2.4	104.4	2.0
	(29)	(29)	(30)	(20)	(18)	(18)
Apr.	265.7	20.9	271.8	2.0	96.8	1.3
	(33)	(33)	(31)	(22)	(30)	(20)
May	272.2	29.6	296.0	2.5	104.6	1.2
	(50)	(50)	(37)	(20)	(30)	(20)
June	273.8	28.0	286.5	2.4	99.7	0.9
	(27)	(15)	(35)	(15)	(30)	(15)
		35.9[c]				
		(12)				
July	299.9[d]	4.9			104.0	1.0
	(30)	(15)			(30)	(20)
Sep.	300.1	5.3	301.2	2.8	106.2	1.1
	(29)	(20)	(30)	(15)	(30)	(15)
Nov.	285.5	6.5	288.5	3.0	102.2	1.4
	(30)	(30)	(30)	(15)	(30)	(15)
Dec.	297.9	10.7	308.9	2.5	103.1	1.6
	(30)	(30)	(30)	(15)	(30)	(15)
Feb.	294.2	15.0	287.3	2.1	101.1	2.1
	(30)	(30)	(30)	(15)	(30)	(15)

[a]Approximate 95% confidence intervals are ±3% for body weights and ±15% for gonad weights.
[b]In spawning season, values are for ripening or ripe fish only.
[c]These ovaries were very ripe.
[d]Sample might include some immature females because of difficulty of distinguishing spent from immature ovaries.

sample averages; most samples of males of this size range from St. Margaret's Bay would contain at least 80% mature fish.

Spawning in 1970 occured from April to June, with a probable peak late in May. Ovary weights of mature females reached a maximum in May and examination of the complete trawl catches indicated that fish with ripe ovaries (Pitt 1966) were present in relatively smaller numbers by the end of June and were virtually absent at the end of July.

Ovary weights of American plaice at spawning were relatively larger in big fish. In May, 1970, the ovaries of 50 fish were examined and ovary weight (w_{ov}, in grams) was found to be related to gutted weight (w, in grams) by the regression

$$w_{ov} = 0.0252\, w^{1.261}$$

The exponent is significantly different ($P < 0.05$) from 1.0. The ovary weight of a fish weighing 150 g constituted 9.3% of the gutted weight whereas that of a 500 g fish was 12.7% of the weight.

Percent dry weights — Percent dry weights of body materials for all three sample categories (Table 2) were lowest in April and highest in September. The values for both mature and immature females ranged from 18 to 22% and those for males from 20 to 23%.

The percentage dry weight of mature female ovary materials was closely related to stage of development in the annual reproductive cycle. Percent dry weight increased continuously from 15% for spent ovaries in July to 27% for ripening ovaries in February and remained near 27% as further ripening took place in the last few months before spawning.

During the final stages of ovary maturation prior to spawning the percent dry material decreased and the ovary wet weight increased considerably. In the sample of June, 1970, similar numbers o

TABLE 2. Percent dry weights (*g*) of the body and gonad materials.[a]

Month	Mature females (*30–40 cm*)[b]		Immature females (*30–40 cm*)		Males (*20–30 cm*)	
	Body	Ovary	Body	Ovary	Body	Testes
Mar.	18.5±0.6 (15)	27.0±0.7 (19)	18.2±0.4 (19)	14.0±0.4 (18)	–	11.1±0.5 (17)
Apr.	17.7±0.6 (23)	27.7±0.5 (23)	18.3±0.5 (22)	14.9±0.6 (22)	20.2±0.5 (20)	10.1±0.5 (20)
May	18.4±0.3 (17)	27.0±0.4 (17)	19.4±0.5 (20)	13.9±0.6 (10)	20.2±0.6 (20)	12.1±0.5 (20)
June	19.3±0.6 (20)	25.6±0.4 (15)	20.0±0.4 (15)	15.6±0.3 (15)	20.5±0.6 (15)	11.9±0.7 (15)
	–	17.6±2.8[c] (12)	–	–	–	–
July	20.4±0.4 (15)	15.2±0.6 (15)	–	–	22.0±0.7 (20)	11.4±0.9 (20)
Sep.	22.6±0.5 (15)	17.0±1.4 (15)	21.8±0.6 (15)	15.0±0.7 (15)	23.4±0.5 (15)	14.0±0.7 (15)
Nov.	21.1±0.5 (15)	19.8±1.4 (15)	20.1±0.7 (15)	14.6±0.6 (15)	21.2±0.5 (15)	14.8±0.7 (15)
Dec.	21.7±0.5 (15)	22.4±1.3 (15)	21.4±0.7 (15)	14.5±0.4 (15)	22.6±0.5 (15)	11.8±0.6 (15)
Feb.	20.7±0.3 (20)	27.0±0.9 (20)	20.4±0.5 (15)	15.0±0.5 (15)	21.2±0.5 (15)	12.0±0.3 (15)
Mean	20.0	22.7	19.9	14.6	21.4	12.2

[a]Figures are sample means with 95% confidence intervals. Number of replicates are given in brackets.
[b]Values apply to fish throughout the range in length.
[c]These ovaries were very ripe.

fish with ripening (stage IIIA) and very ripe (stage IIIC) ovaries were obtained. The ovary wet weights computed for 35-cm females (Table 1) were 28.0 and 35.9 g, respectively, and the corresponding values for percent dry material (Table 2) were 25.6 and 17.6%.

The percent dry weight of immature ovary material during the year was 15 ± 1% while the percent dry weight of testes material was 12 ± 2%.

On two occasions head samples amounting to about 25% of gutted weight were analyzed and the percent dry weights were 17.4 ± 0.4% for 35-cm females and 19.6 ± 0.5% for 25-cm males.

Percent dry weights of viscera materials, which constituted about 4% of gutted weight, were determined on occasions during summer and winter for females and males. Values were 18.5 ± 0.5% in May and 19.5 ± 0.9% in November for females and 23.3 ± 1.2% in July and 19.2 ± 0.5% in February for males.

Energy per unit dry weight — The seasonal patterns of energy per unit dry weight of all materials (Table 3) were similar to the patterns for percent dry weight, but energy content values in most cases did not vary beyond ±5% of the annual average value for each type of material.

The calorific value of head materials was 4088 ± 224 cal/g dry weight for females and 4430 ± 332 cal/g dry weight for males.

Viscera material from females contained 5055 ± 264 cal/g in May and 5105 ± 152 cal/g in November; that from males, 5313 ± 392 cal/g in July and 5105 ± 159 cal/g in February.

Seasonal Energy Storage Patterns

The seasonal energy storage pattern (Fig. 1) for a standard length fish was constructed from estimated values for energy of components of the fish at successive times of the year. Total energy of the fish, E, was evaluated with the expression

$$E = E_h + E_b + E_v + E_g$$

where E_h = energy stored in the head, E_b = energy in the body less gonads, E_v = energy in viscera, and E_g = energy in the gonads.

Head samples from 15 females constituted 27% of gutted weight including gonads while heads from 20 males amounted to 24% of gutted weight. Since 25 cm females weigh about 300 g and 25 cm males about 100 g it is reasonable to assume average head weights of 75 and 25 g and energy contents of 53.4 and 21.8 kcal, respectively. Energy per unit

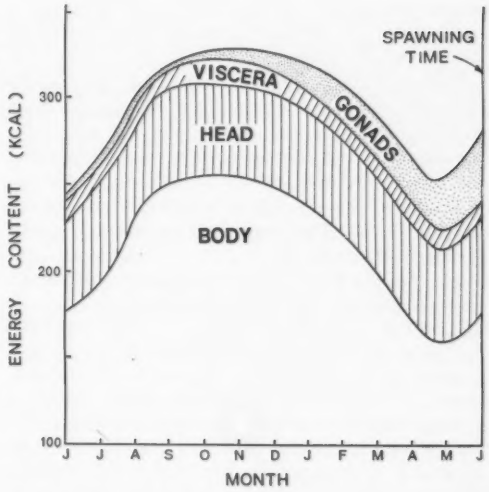

FIG. 1. Seasonal pattern of energy storage in components of a mature 35-cm female American plaice from St. Margaret's Bay, N.S.

dry weight and percent dry weight values for head materials were given previously.

Energy contents of viscera throughout the year were computed from data on samples of both sexes taken once in summer and once in winter together with assumptions concerning the seasonal pattern of variation. The mean ratio of viscera weight to gutted weight for 40 females on the two sampling occasions was 0.042. Assuming an average body weight of 290 g for a 35 cm fish, the viscera weight was 12.3 g. The mean energy content of the viscera examined was 975 cal/g wet weight and so the mean viscera energy of a 35 cm female can be taken as 12.0 kcal. Variation in viscera energy from this mean value is due largely to seasonal changes in liver weight. Observations on liver weight variation of plaice (J. Smith personal communication) indicate that during the year the range in liver weight amounts to about 1% of gutted weight. For a 35-cm female fish this would mean a liver weight change of 3 g during the year. As a conservative estimate, it was assumed that energy per unit liver weight is the same as that for viscera in general; this indicates a change of 3.0 kcal in the viscera energy of a 35 cm female during the year. The observed pattern of liver weight variation coincided in general with the pattern of body condition; it was assumed that the viscera energy reaches a maximum on November 1 and a minimum on May 1 and that the variation in between is linear. Similar considerations apply to the calculation of viscera

energy for males; observations on 35 fish gave a mean ratio of viscera to gutted body weight of 3.6% and an energy content of 1110 cal/g.

Energy in the body was computed by subtracting the estimated head weights from the gutted body weights (Table 1) and multiplying the remainder by corresponding values of percent dry weight and energy per unit dry weight (Tables 2 and 3).

Energy of the gonads was computed from gonad weights (Table 1) by the procedure described above for body components.

In general, the seasonal pattern of total body energy storage was similar to the pattern of condition defined by body weight at standard length, but the variation was relatively greater in the energy storage pattern. A standard 35-cm mature female, for example, experienced an annual body weight variation of 35 g relative to an average weight of 290 g, while the energy storage variation was 100 kcal and the average total energy 275 kcal. Immature females and males exhibit similar patterns but the ranges of variation are not as large.

Discussion

Energy content of American plaice materials — The energy per unit dry weight values for all American plaice materials (5000 cal/g ± 8%) were consistent with the range 5000 cal/g ± 20% given by Winberg (1956) for all fish species. American plaice contain relatively little fat and it is, therefore, not surprising that the mean calorific value is close to that of protein and that the seasonal variation is relatively small. The energy values for plaice are low relative to recently published values for fish with significant fat cycles. Lasker (1970) gives 1400 cal/g wet weight (or 5600 cal/g dry weight, assuming 25% dry material) for body material of the Pacific sardine (*Sardinops sagax* [= *caerulea*]). Sandercock (MS 1969) found average values of 5740 cal/g dry weight for body material of kokanee (*Oncorhynchus nerka*) and 5600 cal/g for rainbow trout (*Salmo gairdneri*).

The seasonal variation in energy per unit wet weight of plaice (Table 3) was similar to that reported for other species of fish. The greatest changes oc-

TABLE 3. Energy per unit dry weight (*cal/g*) of the body and gonad materials.[a]

	Mature females		Immature females		Males	
Month	Body	Ovary	Body	Ovary	Body	Testes
Mar.	4734±297 (6)	5272±233 (6)	4843±614 (4)	4656±265 (3)	–	5160±306 (4)
Apr.	4662±167 (6)	5190±300 (6)	4816±549 (4)	4448±330 (3)	4617±261 (4)	4707±383 (4)
May	4812±153 (6)	5288±136 (6)	5044±306 (4)	4651±147 (3)	4960±87 (6)	5139±228 (4)
June	4997±161 (6)	5358±125 (6)	4880±234 (6)	4567±271 (3)	4983±403 (4)	5163±274 (4)
	–	5272±267 (6)	–	–	–	–
July	5016±243 (6)	4909±289 (4)	–	–	4915±287 (7)	4970±195 (4)
Sep.	5342±334 (6)	4980±247 (6)	5278±453 (4)	4767±285 (3)	5263±196 (4)	4901±336 (3)
Nov.	4743±316 (6)	4986±228 (6)	4647±285 (4)	4579±597 (3)	4576±138 (4)	4743±420 (3)
Dec.	4914±470 (6)	5043±219 (6)	5129±469 (4)	4892±447 (3)	4902±410 (4)	5020±106 (3)
Feb.	4883±422 (6)	5417±333 (6)	4913±358 (4)	4630±921 (3)	5392±508 (4)	5386±502 (3)
Mean	4900 (54)	5160 (52)	4944 (34)	4649 (24)	4951 (37)	5021 (32)
Cal/g wet wt	980(825–1207)[b]	1171(746–1428)	984(881–1150)	679(647–715)	1060(933–1232)	613(475–702)

[a]Figures are sample means with 95% confidence intervals. Numbers of replicates are given in brackets.
[b]Mean and range.

curred in mature females, the range of variation for body material being 39% of the mean and that for ovary material 58% of the mean. The variation for body materials of immature females was similar to that for males. The variation was least for immature ovaries but was almost as large in testes as in mature ovaries. Mann (1972) reported changes in energy from 850 cal/g to 1150 cal/g during the year for roach (*Rutilus rutilus*) and 870–1450 cal/g for bleak (*Alburnus alburnus*). Sandercock (MS 1969) found annual variations of 870–1360 cal/g in mature rainbow trout (*Salmo gairdneri*) and 725–1490 cal/g in mature kokanee (*Oncorhynchus nerka*) while seasonal changes in energy content of immature fish were somewhat less.

Energy storage and conversion processes — The relations between the annual cycle of energy storage and the processes of ingestion, metabolism, and growth of plaice can be investigated with an energetics analysis. This analysis requires information concerning periods of feeding and growth, timing of events in the reproductive cycle, rates of metabolism and certain energetics efficiencies, together with the conservation of energy equation

$$\frac{dE}{dt} = A - R$$

where dE = change in energy content of an individual fish during a time interval dt, A = net energy intake as assimilated food less energy loss as excretion during the interval, and R = net energy expenditure for metabolism (respiration).

Since American plaice in the Northwest Atlantic region feed very little in winter (Powles 1965) and increases in length occur mainly during summer and fall (Pitt 1967), it can be assumed in an approximate analysis that the feeding–growth period is May 1 to November 30.

In the absence of winter feeding there must be transfer of energy from body to mature ovary since ovary weight and energy increase continuously from the time of recovery from spawning in the summer months until spawning in the following spring. Biochemical considerations (Blaxter 1962) suggest that an energetic efficiency of perhaps 90% for this transfer process would be reasonable.

American plaice are not very active fish and during winter months especially the level of metabolism may be close to standard metabolism values measured in the laboratory whereas during the summer routine metabolism would be somewhat higher than standard metabolism. Values for standard metabolism of plaice at temperatures representative of St. Margaret's Bay are reported in MacKinnon (unpublished data).

Analysis of the seasonal energy storage patterns (Fig. 1) shows that the net decrease in energy during the winter months is approximately sufficient to meet energy requirements for gonad maturation and metabolic maintenance. For 35-cm mature females the decrease in total energy, excluding ovaries, between December 1 and April 30 was 92 kcal. The increase in ovary energy during this period was 18 kcal and, assuming an efficiency of 90%, the decrease in body energy required to meet this requirement was 18/0.90 = 20 kcal. Energy available for maintenance requirements was, therefore, 92 − 20 = 72 kcal, or 14.4 kcal/month. Calculations based on plaice respiration measurements indicated that about 14.3 kcal/month would be consumed in standard metabolism processes.

Of the energy assimilated and stored by a mature American plaice female of 35 cm, a proportion is used for growth associated with an increase in body length. A female plaice of this size in St. Margaret's Bay increases in length by 2 cm and in weight by about 18% during one year (Bakken unpublished data); the corresponding amount of energy storage, assuming an average weight of 290 g during the annual cycle and an average energy content of 980 cal/g, is 290 × 0.18 × 0.980 = 51.2 kcal. During the feeding season a total of 20.7 kcal is stored directly in the ovary: 12.3 kcal prior to spawning and 8.4 kcal during recovery before December. The net increase in energy of the body (excluding gonads) which is not associated with growth in length is 91.5 kcal; as noted above, 20 kcal of this amount is used during winter for ovary maturation and, hence, a total of 40.7 kcal per year is devoted to egg production. The total production of materials by a 35-cm female during the feeding period was then as follows:

Energy storage associated with growth in length	=	51.2 kcal
Energy stored in the ovary before spawning (May 1–May 30) 12.3 kcal after spawning (June 1–Nov. 30) 8.4 kcal total	=	20.7 kcal
Energy storage for winter metabolism and gonad maturation	=	91.5 kcal
Total	=	163.4 kcal

Averaging over the 7 month feeding period this gives a production of 23.3 kcal/month.

The average monthly production values given above are consistent with information reported in the literature on food conversion of flatfish (Pandian 1970; Edwards et al. 1969). These studies indicate that it is reasonable to assume an overall growth efficiency of 30% for a 290 g plaice; this would

give a monthly ingestion rate of 23.3/0.30 = 77.7 kcal. Winberg (1956) has shown that assimilation efficiencies of 80% are appropriate for fish and Kerr (1971) has reviewed evidence that indicates approximately 30% of ingested energy is lost as heat during food processing. The average amount of energy per month for metabolism can then be estimated as follows:

		kcal/month
Energy ingested as food, C =		77.7
Less losses due to egestion and excretion, F + U =		15.5
Energy assimilated, A =		62.2
Less energy losses during food processing (specific dynamic action), 0.30 C =		23.3
Energy remaining for growth, standard metabolism, and activity =		38.9
Growth and summer gonad production	10.3	23.4
Energy storage for winter metabolism and gonad maturation	13.1	
Energy for summer standard metabolism and activity (by difference) =		15.5

Estimated energy expenditure for standard metabolism of a fish this size at temperatures characteristic of St. Margaret's Bay in summer is 14.3 kcal/month according to laboratory respirometer measurements (MacKinnon unpublished data). In these experiments, no significant difference between standard respiration rates of plaice during summer and winter months was detected.

The reasonable agreement between estimates for metabolic expenditures computed from observed changes in energy storage and the laboratory measurements of standard metabolism is support for the essential features of the analysis outlined above. During winter months, energy expenditures for activity are probably minimal since little foraging occurs; accordingly, the maintenance metabolism computed from energy storage changes is approximately equal to standard metabolism computed from respiration measurements. For the summer months, the energy for standard metabolism and activity estimated above from energy changes, 15.5 kcal/month, exceeds the estimate of 14.3 kcal/month for standard metabolism according to respirometer measurements. The difference of 1.2 kcal/month for activity seems reasonable in view of the foraging behavior of plaice but this value must be considered only a rough estimate because of the number of assumptions involved in its calculation.

Energy storage and reproduction — Analysis of the energy changes in mature plaice females suggests that accumulation of energy in the ovary occurs partly during the feeding season and partly during the overwintering period by transfer of energy from other parts of the body. Love (1970) has suggested that the buildup of gonads is often, perhaps always, accomplished at the expense of body proteins. In American plaice it appears that about 50% of gonad energy increase occurs during the winter months when there is a continuous decrease in body energy; the absence of feeding makes it necessary to postulate transfer of energy from body to gonad. During the summer months it is conceivable that energy would first be stored in the body and then transferred to the gonad but it would seem improbable in view of the relative inefficiency of such a process.

Prior to spawning the ovary appears to swell considerably due to incorporation of water. During June 1970, 15 ripening and 12 very ripe ovaries were examined (Tables 1, 2, and 3). The energy per unit dry weight was approximately the same in the two types of ovary. However, the very ripe ovaries had a relatively higher wet weight and a lower percentage dry material than the ripening ovaries. The computed dry weight of material in the ovaries of a 35-cm fish at this time is 7.2 g when in a ripening state and 6.3 g when very ripe. Since the percent dry weight values for the very ripe ovaries ranged from 10 to 23%, it is reasonable to suppose that some eggs were released from the ovaries with the lowest percent dry material and to conclude that there is no significant difference between the dry weights of ripening and ripe ovaries although the latter have a higher wet weight.

The above explanation of energy changes associated with spawning in American plaice differs from the interpretation of spawning energetics of salmon and trout by Sandercock (MS 1969). Sandercock rejected the hypothesis that energy was transferred from body to gonad prior to spawning and postulated that the observed decrease in body energy resulted in part from the demands of migration but was largely due to the metabolic processes associated with significant changes in physiological state which take place near spawning time. It would appear that the complex of energetics processes during the spawning period of American plaice is quite different from that for salmon or trout. Furthermore, it seems clear that the suggestion by Love (1970) concerning buildup of gonads cannot be considered a general proposition.

The amount of energy diverted to egg production in American plaice is relatively greater in larger and older fish, thus supporting the expectation of Williams (1966) that in species which spawn re-

peatedly the intensity of reproductive effort should increase with age. Ovary weight of plaice at spawning time was found to be proportional to body weight raised to a power of 1.26 and, when the energy content of plaice material is considered, the energy in ripe gonads of 150 and 500 g fish constitutes 13 and 17% of total body energy, respectively. The fact that the ripe gonads of fish may constitute a relatively larger proportion of body weight as age increases has been considered earlier (e.g. Orton 1929), but, in the absence of energetics data, it was not possible to show that this involved a relative increase in energy expenditure for reproduction.

Production and storage of materials for spawning and overwintering maintenance of mature American plaice is at least equal to production of materials for overall body growth; in larger fish, production for growth tends to become a minor component of total production while egg production assumes increasing importance. An estimate of this change in production pattern with size can be made by considering the body and gonad growth data for fish of 30 and 40 cm, the extremes of size in the sample category of this study. Production for overwintering can be estimated from the value for a 35-cm fish by assuming a variation with weight raised to the 0.8 power. Although this assumption cannot be proved with the present data, it seems reasonable in view of the fact that metabolic expenditures vary in this manner. The estimated annual production quantities for 30, 35, and 40-cm mature plaice females are:

Fish length(*cm*)	30	35	40
Gutted weight(*g*)	180	290	440
Body growth production(*kcal*)	40.6	51.2	60.4
Egg production(*kcal*)	21.0	38.7	65.8
Production for overwintering; maintenance(*kcal*)	48.8	71.5	99.8
Total production(*kcal*)	110.4	161.4	226.0

These calculations indicate that production for body growth decreases from 37% of total production in the 30-cm fish to 27% in the 40-cm fish. However, egg production increases from 19% of total production in a 30-cm fish to 29% in a 40-cm fish.

An important conclusion regarding fishing strategy that emerges from the above production calculations is that a significantly greater yield would be obtained from the same number of fish by fishing intensively at the end of the summer period rather than distributing effort throughout the year. This conclusion follows from a distinction between "summer production," which occurs during the feeding period, and "net annual production," which amounts to the difference between summer production and the energy expenditures required for overwintering maintenance. At the end of the feeding period, the summer production (excluding gonads) of a 35-cm female, 142.7 kcal, could be harvested by removal at that time whereas only the net annual production, 142.7 − 91.5 = 51.2 kcal, could be obtained by taking the same fish at the end of the overwintering period.

The increased energy requirement for gonad maturation in large, old plaice may give rise to the jellied condition of flesh, involving high water content, as proposed by Templeman and Andrews (1956), and ultimately may be a contributing factor to death as Gerking (1959) suggested. Estimated annual egg production in a large plaice weighing 2000 g is 500 kcal. If one assumes that about 50% of this energy is transferred from body to gonad during a 5 month overwintering period with an efficiency of 90%, the resultant transfer is 55 kcal/month. This is a large amount relative to an estimated standard metabolic requirement of 65 kcal/month and, if the total energy storage prior to overwintering was not quite adequate or if unfavourable feeding conditions were encountered following spawning, the fish might encounter very severe depletion in body energy and a consequent increase in moisture content leading to a jellied condition. Sandercock (MS 1969) found very high water content and corresponding low energy content in ripe kokanee females which died following spawning. Love (1970) observed that larger cod had relatively higher water content and were physically weak when landed. It is therefore possible that larger plaice which undergo greater than average depletion at spawning may have an increased probability of death.

The strategy of summer feeding — Evidence presented in this paper establishes the existence of an energy storage cycle associated with the annual feeding–overwintering–spawning events in American plaice but no direct information is provided concerning the factors which control this cycle. It appears, however, that there is no simple dependence upon environmental variables such as temperature and light. The standard metabolism of plaice is independent of temperature within the range normally experienced by the species in St. Margaret's Bay (MacKinnon unpublished data). Feeding rates of plaice, as well as migratory movements, are not consistently related to temperature; Powles (1965) observed that fish in the Gulf of St. Lawrence move inshore to feed in the spring when temperatures are very cold (−1.8 − 0 C) while overwintering occurs at temperatures (2 − 3 C) which are high relative to the annual average. Spawning time of plaice has been found to be uncorrelated with water

temperature (Pitt 1967). Light intensity in the environment inhabited by plaice has a relatively larger and more regular annual variation than temperature. In view of the postulated widespread occurrence of circannual clocks in organisms (Pengelley and Asmundson 1971), it is possible that such a cycle is present in plaice, with light duration providing the main environmental cue.

The strategy of summer feeding plus an energy storage cycle probably has some advantage to American plaice as a species since it is generally accepted (Nikolsky 1963) that the seasonal cycle of events in the mode of life of fishes has adaptive significance. An assessment of the relative advantages of various feeding strategies can be made by computing the annual energy intake needed for a specified amount of annual growth; better strategies should be more conservative of energy.

When food has a constant availability throughout the year, calculations with a simple metabolism/growth model show that there appears to be no energy conservation advantage in adopting a cyclic strategy with feeding in summer only. In an earlier section, it was shown that estimated energy intake of a 35-cm plaice for a 7 month feeding period is 77.7 kcal/month, giving an annual intake of 544 kcal. A comparable estimate can be made for year-round feeding by assuming that standard and average activity metabolism requirements per month are unchanged, food processing efficiency is constant, and the energy stored for growth in length and gonads is the same. With these assumptions, the energy intake for year-round feeding is 45.3 kcal/month. Gross growth efficiency with the cyclic feeding strategy is 30% in summer and 0% in winter whereas, with year-round feeding, the efficiency is 16% during every month. On an annual basis, however, the two strategies result in the same energy intake and growth efficiency.

In situations where there is a significant seasonal variation in the availability of prey which constitute the food resource, there is an energy conservation advantage to a fish in employing a cyclic feeding strategy. Food availability may vary seasonally with changes in productivity arising from the annual pulse of primary production which is characteristic of temperate waters. Further amplification may be provided by changes in vulnerability to predation. Ware (MS 1971) found that, even when abundance was relatively constant, a tenfold variation in vulnerability to predation occurred during the year as a result of changes in behavioral and physical characteristics of the prey. These experiments concerned animals living in an environment with relatively large annual temperature variations which may have had a major influence on prey availability. However, it is reasonable to postulate that seasonal variations in vulnerability are of general occurrence and that suitable mechanisms exist to produce these variations in a constant temperature environment such as that inhabited by plaice. Foraging costs to an individual fish per unit energy intake may be significantly higher during winter months when food availability is relatively low. This additional energy expenditure for winter foraging would make the annual energy intake greater than in the previous case of year-round feeding and constant food availability. It follows that a strategy involving summer feeding only has an energy conservation advantage when food availability varies and has a summer maximum.

An alternative explanation of the cycle is that it evolved in an environment where cyclic operation was imposed and that, in the present relatively constant temperature environment, the mechanism has been retained but the adaptive significance has been lost. This alternative, however, seems less probable than that of a cycle caused by seasonal variation in food availability.

In addition to possible increases in efficiency of energy use, a biological system with a cyclic mode of operation attains greater stability in situations where there are fluctuations in the energy (food) supply (Sollberger 1965). An organism without an energy storage capacity is constantly dependent upon energy flow from its food resource for its survival; any significant interruption in this flow will result in death. When energy can be stored, the organism attains increased homeostatic capacity (i.e. stability) which allows it to survive periods of interruption in energy flow from its food supply. This homeostatic capacity would be of considerable value to a fish in an environment where the food supply varied seasonally to such an extent that during winter months availability would very probably attain levels equal to or less than the fish's maintenance requirements. Under these circumstances, a storage capacity would be necessary to survive periods of several months when the mean level of food availability is below maintenance as well as shorter periods of very low food abundance which might randomly occur.

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NOTES

Size Selection of *Daphnia pulicaria* by Yellow Perch (*Perca flavescens*) Fry in West Blue Lake, Manitoba

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WONG, B., AND F. J. WARD. 1972. Size selection of *Daphnia pulicaria* by yellow perch (*Perca flavescens*) fry in West Blue Lake, Manitoba. J. Fish. Res. Bd. Canada 29: 1761–1764.

Prior to mid-July, *Daphnia pulicaria* in yellow perch (*Perca flavescens*) fry stomachs were smaller than those in plankton collections but after this date mean lengths of *D. pulicaria* in stomachs and collections were similar indicating an initial selection for small *D. pulicaria* by the fish. The relation between *D. pulicaria* body depth and perch mouth gape width indicated that perch fry less than 18 mm long, a length attained in mid-July, could not readily ingest *D. pulicaria* with body depths greater than 0.7 mm (1.3 mm long). The heterogonic relation between growth in mouth and body size enabled perch fry in West Blue Lake to quickly utilize, as an energy source, the abundant *D. pulicaria* population.

WONG, B., AND F. J. WARD. 1972. Size selection of *Daphnia pulicaria* by yellow perch (*Perca flavescens*) fry in West Blue Lake, Manitoba. J. Fish. Res. Bd. Canada 29: 1761–1764.

Avant la mi-juillet, les *Daphnia pulicaria* trouvés dans les estomacs d'alevins de perchaude (*Perca flavescens*) sont plus petits que ceux des échantillons de plancton. Cependant, après cette date, les daphnies sont de même taille dans les estomacs et dans les collections, ce qui démontre, chez les alevins, une sélection initiale des petits *D. pulicaria*. La relation entre la hauteur du corps de *D. pulicaria* et la grandeur de l'ouverture de la bouche de la perchaude indique que les alevins mesurant moins de 18 mm de longueur, longueur atteinte à la mi-juillet, ne peuvent facilement saisir les *D. pulicaria* dont le corps dépasse 0.7 mm de hauteur (1.3 mm de longueur). La relation allométrique entre la croissance de la bouche et la grandeur du corps permet aux alevins de perchaude du lac Bleu-Ouest d'utiliser rapidement, comme source d'énergie, l'abondante population de *D. pulicaria*.

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RESULTS presented in this report were obtained as part of a study designed to describe feeding and growth in yellow perch (*Perca flavescens*) fry during their first summer in West Blue Lake, Manitoba (Wong MS 1972). The purpose of this portion of the work, carried out between July 1 and August 25, 1969, was to determine the relation between perch size and the size of their primary prey, *Daphnia pulicaria*.

Previous studies have shown that mouth sizes of different but related species affect the size of prey taken (Northcote 1954) and that, within a species (juvenile rainbow trout), as mouth size increases prey size increases too (Hartman 1958). Other studies have shown that fish frequently select the largest species of zooplankton and, also, the largest individuals of a single species (Brooks and Dodson 1965; Reif and Tappa 1966; Galbraith 1967; Wells 1970; Hutchinson 1971). However, food size selectivity by the often abundant fry of common freshwater fish species has seldom been considered.

Materials and methods — West Blue Lake is a relatively deep (mean depth 11.3 m, maximum depth 30 m), multibasin lake lacking an outlet and permanently flowing inlet streams (Bell and Ward 1970). The only two abundant fish species are yellow perch and walleye (*Stizostedion vitreum vitreum*). During early and mid summer perch fry occupy the epilimnion, where they are the predominant plankton-feeding fish species, almost exclusively consuming *D. pulicaria*. Walleye fry are

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rarely captured in this zone (Wong MS 1972). In mid-August the fry occupy the littoral zone but continue to feed on *D. pulicaria*. *Daphnia pulicaria* (originally identified as *D. pulex*) is the principal zooplankter in terms of biomass during summer. Other abundant species are *Cyclops bicuspidatus* and *Diaptomus siciloides* (Bell and Ward 1970).

Between July 1 and August 10, 1969, age 0+ perch fry were captured at weekly intervals using a hoop net (1-m diameter) towed at the surface between two boats at a speed of approximately 4 km/hr. Tows of 5 min duration were made over the deepest portions of the lake between 1900 and 2400 hr. Later in summer, when perch fry inhabited the littoral zone, they were collected using a fine mesh seine.

All collected fish were killed immediately and preserved in 5% formalin. The total length of each fish under 20 mm was measured to the nearest 0.1 mm using a dissecting microscope fitted with a measuring eyepiece and a stage micrometer. Larger fish were measured to the nearest 0.5 mm with a ruler. Width of mouth gape (Hubbs and Lagler 1958) of perch fry was measured with a brass cone (11°25′ taper) and calibrated in 0.2-mm increments.

In small fry, prior to formation of the stomach, food in the full length of the digestive tract was examined but in older fish only the esophagus and the stomach contents were analyzed. *Daphnia pulicaria* found in perch stomachs, and those sampled from the lake, were separated (Ward et al. 1970) into 13 length classes, each with an interval of 0.2 mm. The depth of *D. pulicaria* found in perch fry stomachs was measured along the maximum dorso-ventral axis.

The *D. pulicaria* population was sampled at Station 2 (Bell and Ward 1970) at 5-m intervals throughout the water column (30 m) using a 4-liter Van Dorn sampler. Samples were collected at 2-week intervals during the spring and summer of 1969.

Results — In early July mean lengths of *D. pulicaria* found in perch stomachs were considerably less than mean lengths in plankton samples (Fig. 1). For instance, the mean length of *D. pulicaria* in stomachs on July 1 was approximately 1.0 mm in contrast with 1.6 mm for animals in the plankton. The largest *D. pulicaria* present in the lake (2.6 to 3.0 mm) were rarely found in stomach contents until mid-August (Fig. 1). By and subsequent to July 15, mean lengths of *D. pulicaria* in perch stomachs and in plankton samples were approximately equal, although mean sizes in stomachs were always less than in plankton samples, perhaps because of "packing" in the gut.

The relation between perch gape width and *D. pulicaria* body depth (Fig. 2) indicated an initially rapid increase in the depth of *D. pulicaria* eaten. The inflection, occurring at gape width 1.9 mm, corresponded to a perch length of approximately 18 mm and to a *D. pulicaria* body depth of about 0.7 mm (1.3-mm body length). Perch did not attain this length until mid-July and the average length of *D. pulicaria* in perch stomachs was less than 1.3 mm until mid-July also.

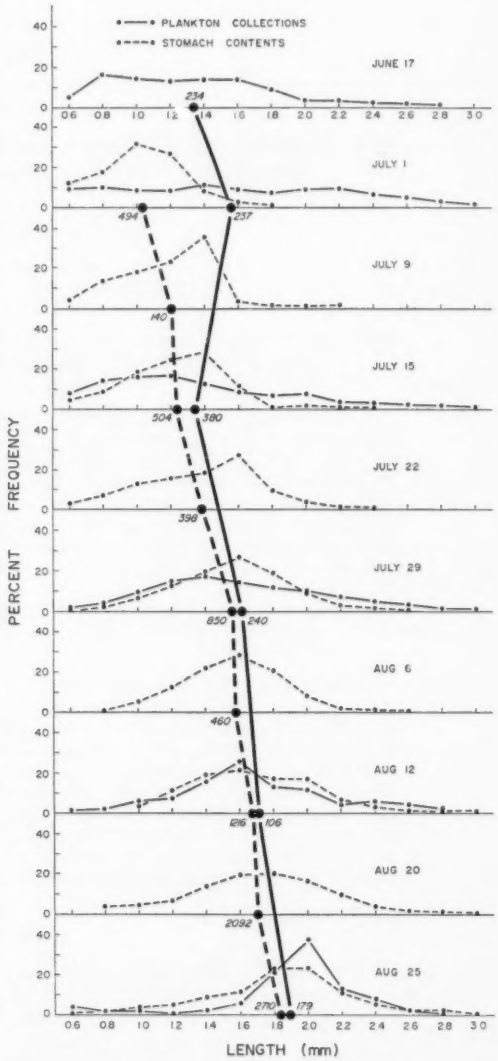

FIG. 1. Length distributions and mean lengths of West Blue Lake *Daphnia pulicaria* in plankton collections and in perch fry stomachs during the summer of 1969. Numerals near points representing mean lengths are numbers of *D. pulicaria* measured.

Ratios of gape width to body length in perch fry (Fig. 3) indicated that mouth size increased more

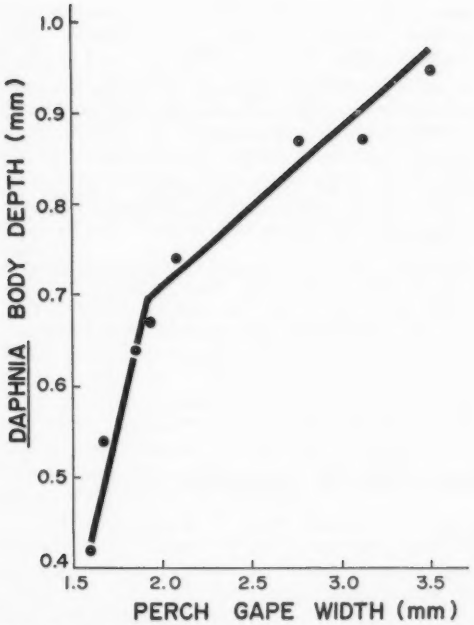

FIG. 2. Relation between perch mouth gape width and body depth of *D. pulicaria* found in perch stomachs during the summer of 1969. A total of 771 perch fry were measured.

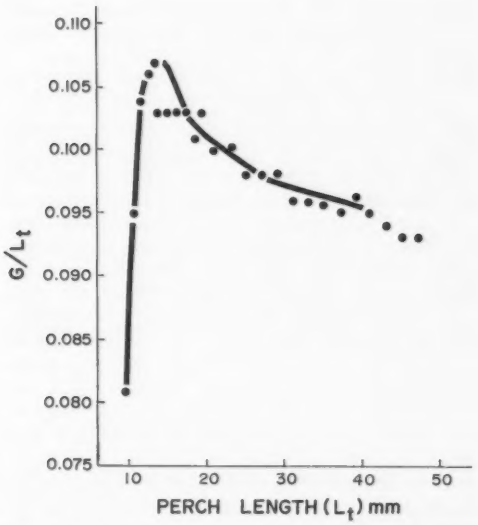

FIG. 3. Relation between ratio of perch gape width (G) to total length (L_t) and perch total length determined from 348 fish sampled during the summer of 1969.

rapidly initially than did body length. The ratio reached a maximum at a fish length of about 13 mm.

Discussion — The initial differences between *D. pulicaria* in perch stomachs and in plankton collections (Fig. 1) indicate perch selectivity for small *D. pulicaria*. The relation between *D. pulicaria* body depth and perch gape width (Fig. 2) also indicates an initial selection for the smaller cladocerans. Apparently, *D. pulicaria* longer than 1.3 mm could not be readily ingested by perch fry until mid-July, when they had attained a total length of approximately 18 mm. Perch fry between 20 and 25 mm, feeding on *D. pulicaria* in an aquarium, rarely seized large specimens but when they did they usually released them. These observations, too, indicate that small perch fry do not ingest the largest cladocerans present in the lake in early summer and, therefore, predation tends, initially, to select the smaller individuals.

Ratios of gape width to body length in perch fry (Fig. 3) indicated that growth in mouth size was more rapid than growth in body length. This heterogonic relation between mouth and body growth permitted early utilization of relatively large food items.

Daphnia pulicaria, the predominant zooplankter in West Blue Lake during summer, is generally larger than either of the common copepods, *Diaptomus siciloides* and *Cyclops bicuspidatus*. Full utilization of the *D. pulicaria* population by perch fry early in their life might permit rapid growth and relatively high survival rates.

Fish have been reported to select the large zooplankton species and individuals (Brooks and Dodson 1965; Galbraith 1967) but in West Blue Lake, prior to mid-July, perch fry select small *D. pulicaria*. This size selective predation occurs during a relatively brief period of approximately 3 weeks following hatching.

Acknowledgments — We thank Dr J. R. M. Kelso and Mr M. R. Falk for their suggestions and assistance in sampling. The Manitoba Department of Mines, Resources, and Environmental Management and the Fisheries Research Board of Canada provided financial support through grants to F. J. Ward.

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Sea Lions Wintering Along the Outer Coast of Vancouver Island

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SMITH, I. D. 1972. Sea lions wintering along the outer coast of Vancouver Island. J. Fish. Res. Bd. Canada 29: 1764–1766.

Aerial counts conducted on the north and west coasts of Vancouver Island during four periods in the 1970–71 winter indicated that more than 1980 sea lions used a total of 15 haul-out areas. Evidence is presented indicating that many winter haul-out areas are often deserted in summer.

SMITH, I. D. 1972. Sea lions wintering along the outer coast of Vancouver Island. J. Fish. Res. Bd. Canada 29: 1764–1766.

Des recensements aériens effectués sur les côtes nord et ouest de l'île Vancouver à quatre époques au cours de l'hiver 1970–71 révèlent que plus de 1980 otaries se réunissent à terre en 15 endroits différents. L'auteur démontre que plusieurs aires occupées en hiver sont souvent désertes en été.

Received April 4, 1972

THIS note presents the results of aerial counts of sea lions along the north and west coasts of Vancouver Island during the winter and early spring of 1970–71. Although a number of reports have been made of summer concentrations along the British Columbia coast (Newcombe and Newcombe 1914; Newcombe et al. 1918; Wailes and Newcombe 1929; Pike and Maxwell 1958; Pike and MacAskie 1969), there has been no previous attempt to describe the winter distribution of the colonies.

Because of size and coloration, I believe that the majority of animals counted were Steller's sea lions (*Eumetopias jubatus*), although some may have been California sea lions (*Zalophus californianus*), which have been reported south of the 49th parallel in Barkley Sound and at Race Rocks (Cowan and Guiguet 1965; Hancock 1970).

Pike and Maxwell (1958) reported summer haul-out areas off the northern tip of Vancouver Island, Solander Island, and Cape Cook; and the west coast of Vancouver Island south of Cape Cook. While their account was not specific on this point, I know of no haul-out area on Cape Cook and thus suspect that they were referring to a large number of sea lions which inhabit rocks just to the south of Cape Cook, in Checleset Bay. Sea lions are also com-

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monly known to occur off Long Beach in summer, and I have observed 5–10 sea lions at Carmanah Point in late August. Gordon Smith of the British Columbia Fish and Wildlife Branch has told me of seeing concentrations of sea lions in summer at Folger Island while Wayne Campbell, curator of the vertebrate museum of the University of British Columbia, has seen sea lions at both Cleland and Wouwer islands in summer. However, all three of these islands are often deserted during the summer months.

No other summer haul-out locations have been reported.

The counts reported here resulted from four flights which were made over various parts of the coast. It was impossible to cover all sections of the coast in a single flight since the census was conducted in conjunction with other activities. The flights were designed to cover the haul-out areas noted above, plus other likely unknown haul-out areas along the outer coastline.

All results were based upon 35-mm color slides taken from a height of 300 ft or less, with the exception of the area between Race Rocks and Pachena Point, which was not photographed during the November 27 flight.

Results of the flights (Table 1) indicated that more than 1980 sea lions used 15 haul-out areas (Fig. 1) along the north and west coasts of Vancouver Island during the winter of 1970–71. Three of the haul-out areas (Sombrio Point, Rafael Point, and Ferrer Point) had not been previously reported.

The estimate of more than 1980 sea lions was derived by totalling the largest count recorded at each haul-out area, on the assumption that Vancouver Island sea lions are site-specific aside from periods of migration. If so, the large variations in numbers of sea lions observed at given locations must have been due to animals being at sea rather than animals shifting to other colonies.

Because of adverse weather and crowding of the animals, and because some sea lions usually dove into the water before adequate photographic coverage was obtained, the counts in most cases underestimated the actual numbers of animals which occurred at the various colonies, although the degree of error was not believed serious. Only at four locations (Pachena Point, Folger Island, and Wouwer Island on November 27, and Solander Island on February 20) were the recorded totals likely to be seriously in error, as indicated by Table 1. The Pachena estimate was made without the aid of photographs, while in the other three cases large numbers of sea lions were observed leaving the haul-out area before a picture could be taken.

The counts also suffer from the probability that sea lions were absent from some normal haul-out areas during the flights, and that, despite attempts to cover all likely haul-out locations, it is possible that concentrations of sea lions were missed in some areas.

TABLE 1. Aerial counts of sea lions along the north and west coast of Vancouver Island during the winter and early spring of 1970–71. Only counts marked with asterisk represent possible serious underestimates.

Location	Counts during census period				Largest count
	Nov. 27	Feb. 18–20	Mar. 8	Mar. 31	
Race Rocks	50–80				50–80
Sombrio Pt.	50–80				50–80
Carmanah Pt.	2	0			2
Pachena Pt.	100+*	0			100+*
Folger Is.	40+*	51			51
Wouwer Is.	40+*	200+			200+
Long Beach	155+	227+			227+
Cleland Is.	75+	94+			94+
Rafael Pt.		250+			250+
Ferrer Pt.		151			151
Checleset Bay		244+	305		305
Solander Is.		35+*	88		88
Beresford Is.				94	94
Sartine Is.				97	97
Triangle Is.				221+	221+
Total	512+*	1252+	393	412+	1980+

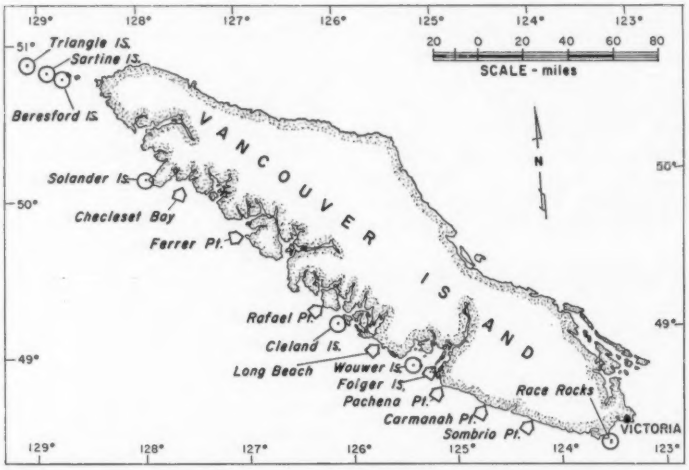

FIG. 1. Fifteen haul-out areas along the north and west coasts of Vancouver Island used by more than 1980 sea lions during the winter of 1970–71.

The counts indicated that all major summer haul-out areas were occupied in the winter of 1970–71, presuming that the reference by Pike and Maxwell to Cape Cook actually refers to the Checleset Bay colony just south of Cape Cook. However, there are strong implications that the converse is not true. Hancock (1970) reports that California and Steller's sea lions occupy the Race Rocks site only from late October until late May, and it is commonly known that the Pachena Point sea lions may usually be observed only from mid-September until early May. As described above, other winter haul-out areas such as Folger Island are also commonly reported to be deserted in the summer months, although animals appear to occupy them sporadically.

Acknowledgments — I wish to thank the following people for their kind assistance in the preparation of this note: M. Bigg and I. MacAskie of the Fisheries Research Board; J. Bandy and G. Smith of the British Columbia Fish and Wildlife Branch; D. Hatler and W. Campbell of the University of British Columbia; and T. Anderson of the Department of Transport. The counts were conducted in conjunction with other activities financed by the British Columbia Fish and Wildlife Branch.

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An Instrument for Measuring Conductivity Profiles in Inlets

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FARMER, D. M., AND T. R. OSBORN. 1972. An instrument for measuring conductivity profiles in inlets. J. Fish. Res. Bd. Canada 29: 1767–1769.

An instrument is described for obtaining profiles of seawater conductivity in the upper few meters of estuarine waters. The system is self-contained and runs for one week between chart replacements; it is housed in a buoy which can be moored to a log-boom or floating dock. Contours of constant conductivity derived from the chart records have provided a graphic description of wind effects in Alberni Inlet.

FARMER, D. M., AND T. R. OSBORN. 1972. An instrument for measuring conductivity profiles in inlets. J. Fish. Res. Bd. Canada 29: 1767–1769.

On décrit un appareil capable de définir les profiles de conductivité de l'eau de mer dans les quelques mètres supérieurs des eaux d'estuaires. L'appareil est autonome et fonctionne durant une semaine sans qu'on ait à remplacer le papier enrégistreur; il est placé dans une bouée pouvant être amarrée à une estacade flottante ou à un ponton. Grâce aux enrégistrements continus de cet appareil, on a obtenu une représentation graphique des effets du vent dans l'inlet Alberni.

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THIS is a description of an instrument for monitoring conductivity profiles in the upper few meters of stratified estuarine waters. Measurements of this type provide the basis for studying time-dependent responses to wind, tide, and runoff in inlets and estuaries. Typically, the strong salinity gradient of these waters dominates the density and, also, the conductivity profile; conductivity therefore provides a more reliable indication of density structure than temperature, especially during the autumn and spring.

It should be emphasized that the instrument will not provide really accurate data in the sense to which we have become accustomed using classical methods of observing salinity and temperature. Rather, it was designed to measure the gross effects, such as a thickening of the surface layer by a factor of more than two in a few hours. The data obtained have confirmed the value of the approach for this problem.

Principles of operation — The instrument (Fig. 1) measures the electrical conductivity of sea water at 14 depths by successively interrogating, for 1 min at a time, each of the 14 conductivity probes on the chain. There

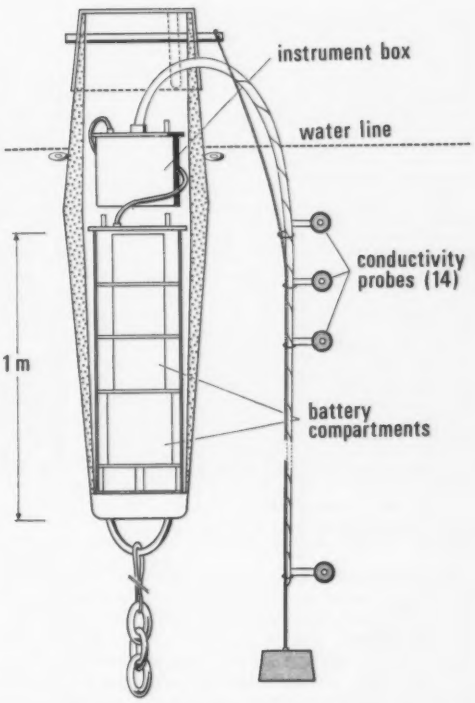

FIG. 1. The conductivity profiling instrument.

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is a 15th probe inside the instrument housing which serves as a check on any drift in the response of the electronics.

Nasmyth (1970) has described the principle used to measure conductivity. Briefly, a 1.5 kHz oscillator supplies a signal to the primary circuit of a toroidal transformer (Fig. 2). The magnitude of the signal induced in the secondary circuit depends upon the electrical conductivity of the seawater loop which surrounds and passes through the center of the transformer. The toroidal probe casing is made entirely of plexiglass. Figure 2 shows how the parts are sealed together using ethylene dichloride in a hypodermic syringe; Fig. 3 shows the completed probe in position.

A Mauthe hobbyist's clock (Fig. 4) controls the timing. This inexpensive unit has an accuracy of better than 4 min/week. A phototransistor in the clockface and a small lamp just above it are so mounted that once each minute the clock's second hand cuts the light path between the two. The phototransistor fires a Schmidt Trigger, which operates the counting logic and switches the appropriate probe into the circuit.

Output from the conductivity measuring circuit is fed to a Rustrak chart recorder (Fig. 5). This type of record has to be laboriously digitized but was chosen in place of a magnetic tape for reasons of cost, simplicity, reliability, and availability.

The deepest probe is interrogated first, then the next deepest and so on. In this way the depth corresponding to a particular reading can be found from the position of the reading relative to the rest of the group on the chart. An event recorder is switched on with the eighth probe and thus serves as a check on the probe sequence. Figure 5 shows the chart recorder with typical output on it.

Instrument housing and protection — Watertight containers of P.V.C. tubing separately house the batteries and the electronics (Fig. 1). Four low specific gravity, 6-volt, lead-acid batteries provide power. A converted fiberglass marker buoy with a lid at one end and an inner sheath of plastic foam affords shock protection and floatation for the battery and instrument cases.

This arrangement permits fairly easy servicing from a small vessel. The batteries were recharged every two weeks and the chart-paper was replaced every week. When replacing the chart-paper alone, it was possible to lift the instrument box out of the buoy and on to the ship's deck since there was a sufficient length of cable to the battery case. Battery replacement required the use of the ship's winch to lift the battery container on board. At all times the buoy remained moored to the log-boom or floating dock to which it was attached.

Calibration — Each probe was calibrated by immersing it in a large container of salt water of known temperature, for which the conductivity could be determined accurately by other means. After noting the output, the cell was removed from the salt solution and a conducting loop in series with a potentiometer was passed through the probe. In this way, it was possible to find a cell constant, Kc, in terms of the solution conductivity, Sc, and the "equivalent resistance", Req, of the potentiometer that yielded the same output as that obtained with the cell in solution; that is,

$$Kc = Req \cdot Sc$$

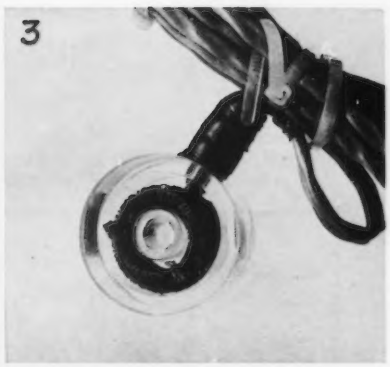
The cell constant is independent of the solution conductivity or the electronics response, being determined solely by the geometry of the cell casing. In practice it was determined by averaging several such calibration measurements. Having found the cell constant, the actual output reading corresponding to different conductivities is found by simply adjusting the potentiometer through a range of values and recording the output. The reading on the chart recorder depends almost linearly on the conductivity being measured.

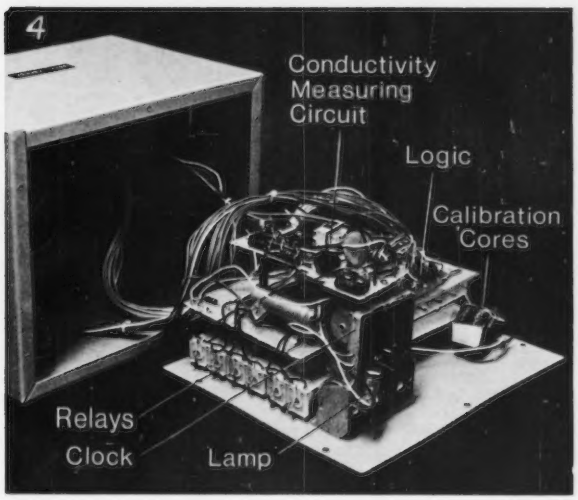
Nasmyth (1970) quotes a short term relative sensitivity better than or equivalent to 0.005 σ_t, and a shift in absolute accuracy over three weeks of 0.07 σ_t, where σ_t is defined as $(\rho - 1) \times 10^3$ and ρ is the seawater density at atmospheric pressure. No such high level of accuracy was sought with the present instrument, although it should presumably be attainable since the conductivity measuring part is basically similar. σ_t calculations require a knowledge of temperature, which was not measured. Moreover, the Rustrak chart recorder limits the repeatability of a single measurement to about one part in a hundred. The recorded output had an estimated relative accuracy between probes of better than $\pm$ 1 millimho/cm and an absolute accuracy better than 2 millimho/cm. The range measured was from a little over 0 millimho/cm to about 35 millimho/cm.

Processing the observations — Each chart record was digitised, punched onto paper-tape, and transferred to magnetic tape on a computer at the University of British Columbia. It was then converted back into conductivity using the relation established by the calibration procedure.

This procedure results in a three-dimensional array of points, the respective axes being depth, time, and conductivity. By interpolating between the points, contours of constant conductivity may be drawn on a plot of depth against time. The result is a graphic description of the detailed changes occurring in the measured water column.

Figure 6 shows one such plot from data taken near Hohm Island in February 1971. The contours clearly demonstrate the sudden thickening of the surface layer associated with strong up-inlet winds on February 14 and, also, the internal tidal oscillation. The vertical spread of contours is indicative of the different degrees of mixing present. For example, the stratification is more intense during that part of the internal tidal oscillation (peaks on the diagram) during which the surface layer is thinnest than during the part at which it is thickest (troughs on the diagram).





FIGURES 2–5

FIG. 2. Sealing the toroidal casing with ethylene dichloride. FIG. 3. Completed probe in position. FIG. 4. Layout of instrument electronics. FIG. 5. Rustrak chart recorder showing typical output.

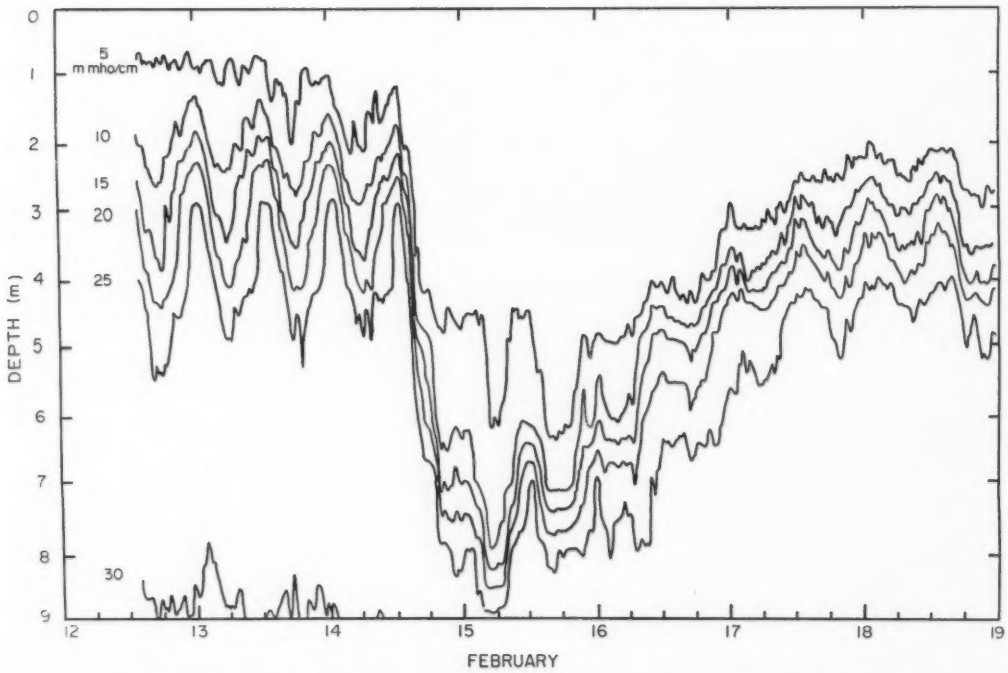


FIG. 6. Contours of constant conductivity derived from the conductivity measurements in Alberni Inlet.

Conclusions — The conductivity profiles provide a simple and efficient means for monitoring the structure of surface water in estuaries and inlets.

The instruments are particularly suitable for measurements in regions of intense salinity stratification where the influence of temperature on the conductivity profile is not great. These conditions prevail in Alberni Inlet where a detailed picture of hourly changes in the density structure of the upper 9 m was obtained.

Acknowledgments — We are grateful to R. W. Chappel for providing us with the conductivity measuring circuit and to Dr R. Parker, Biological Station, Nanaimo, B. C., for providing facilities from his own program in Alberni Inlet, which enabled us to carry out our observations. This work was supported by the National Research Council and by the Marine Sciences Branch and the Fisheries Research Board of the Department of Environment.

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Salmon-Canning Waste Water as a Microbial Growth Medium

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STRASDINE, G. A., AND J. M. MELVILLE. 1972. Salmon-canning waste water as a microbial growth medium. J. Fish. Res. Bd. Canada 29: 1769–1771.

Salmon-canning waste water was shown to support the growth of six species of bacteria both as a complete growth medium and as a supplementary source of available nitrogen. On this basis, the waste water compared favourably to six commercially available sources of nitrogen used routinely in microbiological growth media. Possibilities are discussed for the microbiological conversion of salmon-canning wastes into useful and marketable products.

STRASDINE, G. A., AND J. M. MELVILLE. 1972. Salmon-canning waste water as a microbial growth medium. J. Fish. Res. Bd. Canada 29: 1769–1771.

Les eaux résiduaires de conserveries de saumon favorisent la croissance de six espèces de bactéries, soit comme milieu complet de croissance, soit comme source supplémentaire d'azote. Sous ce rapport, les eaux résiduaires se comparent avec avantage à six sources d'azote trouvées sur le marché et communément utilisées dans les milieux de croissance microbiologiques. Nous discutons des possibilités de convertir microbiologiquement les eaux résiduaires de conserveries de saumon en produits utiles et vendables.

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THE microbial conversion of industrial wastes into marketable products is a concept frequently considered and often implemented in pollution abatement systems. The microbial production of ethanol from waste sulfite liquors (Watson 1959), single cell protein (SCP) from corn oil wastes (Johnson 1968), vitamin B_{12} production from cheese whey (Bullerman and Berry 1966), and the conversion of methane to SCP (Ribbons 1968) are but a few examples.

The purpose of this study is to determine the suitability of salmon-canning waste water as a microbiological growth medium based upon its ability to support the growth of various species of bacteria both as a complete medium and as a supplementary source of available nitrogen.

Materials and methods — The salmon-canning effluent (SCE) was collected from the outfall of a local cannery situated on the south arm of the Fraser River, B.C. The average flow from a plant of this type is about 1135.5 liters/min (Claggett and Wong 1968). The SCE samples used in this study had a total solids content of 1.91 mg/ml after clarification by filtration through glass wool. Although both flow and total solids content vary considerably between samples (Claggett and Wong 1968), total nitrogen and total carbohydrate values are

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TABLE 1. Cell yield as a function of nitrogen source for various species of bacteria.

N-source	Cells/ml of media (log_{10})						
	SCE	Trypticase	Acidicase	Polypeptone	Peptone	Phytone	Meat extract
Sorangium sp.	10.08[a]	6.99	9.51	9.37	9.23	8.29	8.68
P. putrefaciens	9.32	6.38	7.00	8.15	5.30	8.36	8.28
L. plantarum	8.18	7.88	5.30	8.11	9.18	7.26	6.46
A. aerogenes	8.67	7.96	7.79	9.63	9.00	9.04	9.57
Bacillus sp.	7.00	8.65	8.15	8.08	7.63	7.83	7.18
St. faecalis	7.79	7.04	7.30	8.69	7.72	8.23	7.63

[a]Underlined values indicate maximum cell yield.

relatively constant when expressed on a dry weight basis. In the present study the SCE contained 79.5 μg nitrogen and 14.2 μg carbohydrate/mg of solids. All carbohydrate was accounted for as reducing sugar, of which 28% was free glucose.

SCE media — Crude waste water was filtered through glass wool (coarse grade) and 50-ml samples dispensed into 250-ml erlenmeyer flasks. SCE-salts media (SCE-S) was prepared by the addition of K_2HPO_4, 0.2%; $MgSO_4 \cdot 7H_2O$, 0.02%; $FeSO_4 \cdot 4H_2O$, 0.002%; $MnSO_4 \cdot 4H_2O$, 0.002%; and dextrose, 0.5%, to SCE media. The *p*H of the media after sterilization was 7.0–7.1. The following commercially available nitrogen sources were used to evaluate the growth promoting ability of SCE: trypticase (enzymatic digest of casein), Baltimore Biologicals Ltd. (B.B.L.), Maryland; bacto-peptone (enzymatic meat digest), Difco Laboratories, Detroit, Michigan; polypeptone (enzymatic digest of meat and casein), B.B.L.; phytone (enzymatic digest of soya), B.B.L.; acidicase (acid hydrolyzed casein), B.B.L.; beef extract, Difco. These were substituted for SCE at the same final concentration of 1.91 mg dry wt/ml in the SCE-S media.

Six species of bacteria were chosen on the basis of being representative of those types which may be of commercial value and in which we have some current interest. *Sorangium* 495 was obtained from Dr F. D. Cook, Department of Soil Science, University of Alberta; *Pseudomonas putrefaciens* and *Aerobacter aerogenes* were obtained from the Department of Microbiology, University of B.C.; *Lactobacillus plantarum* ATCC 8014; *Streptococcus faecalis* ATCC 7080; and a species of Bacillus designated IR3 was isolated in this laboratory from a local salmon-canning effluent holding-basin. All strains with the exception of *L. plantarum* were maintained on brain–heart infusion agar (BHI) slants. *Lactobacillus plantarum* was maintained on tomato juice agar (B.B.L.). Three separate subcultures (16 hr at 30 C) were made in the appropriate medium prior to the estimation of cell numbers. Serial dilutions of the cultures were plated in triplicate on BHI agar and only plates containing 30–300 colonies were counted.

Total carbohydrate was determined by the method of Morris (1948) and reducing sugar by the method of Somogyi (1945). Free glucose was estimated with the glucostat-reagent (Worthington Biochemicals). Total nitrogen was estimated exactly as described in Official Methods of Analysis (1965).

Results — The data shown in Table 1 indicate the total cell yield for each species in glucose-salts media containing the various sources of nitrogen.

Most obvious was the exceptionally high cell yield (1.15×10^{10} cells/ml) of *Sorangium* in media containing SCE as the sole source of available nitrogen. SCE also supported the maximum yield of *P. putrefaciens*. All six species in fact showed relatively good growth in the SCE-salts media; with the exception of polypeptone and possibly phytone this was not true for the remaining nitrogen sources.

The ability of SCE to serve either as a sole or supplementary source of available nitrogen for microbial growth indicates various possibilities for this waste in the field of microbial fermentations. More important, however, is the ability of SCE to serve in the capacity of a complete medium in

TABLE 2. Cell yield of salmon-canning waste water as a function of cell number per milliliter.

	Cells/ml (log_{10})	% of maximum	Media giving maximum growth
Sorangium sp.	9.34	19.1	SCE-S
A. aerogenes	8.60	9.3	polypeptone-S
Bacillus sp.	7.20	3.6	trypticase-S
P. putrefaciens	6.83	0.3	SCE-S
St. faecalis	6.76	1.2	polypeptone-S
L. plantarum	6.74	0.3	peptone-S

which no other additions are necessary. The data shown in Table 2 indicate the ability of the six bacterial species to utilize this waste as a complete medium under the same growth conditions. The SCE medium allowed a favorable growth yield for *Sorangium*, *Aerobacter*, and *Bacillus* species. Although the remaining species were capable of growing on SCE as a complete medium, the cellular yields for these species were probably not sufficiently high to warrant their use commercially, at least under these growth conditions.

Discussion — Based on the above results, two general approaches may be considered for the microbial utilization of salmon-canning waste water. The first and probably the simplest of these would include those possibilities in which the SCE serves as an inexpensive source of available nitrogen for the microbial degradation and/or utilization of nitrogen-deficient wastes. One such waste of local importance is the spent liquor from the sulfite pulping process. Oxidative lagoons containing pulp-mill effluents often require the addition of a source of available nitrogen in order to achieve a greater degree of microbial degradation of the waste material. The addition of SCE to these lagoons might prove a valuable and inexpensive source of this nitrogen requirement. This also holds for more sophisticated processes in which the spent-liquor is utilized for the production of ethanol (Watson 1959), or vitamin B_{12} (Nishikawa et al. 1970). Fruit canning and petroleum wastes can also be considered in this category of nitrogen poor wastes in which their degradation or utilization may be enhanced by the addition of SCE.

The second appr ach for SCE would include those methods designed for the microbial utilization of the waste per se. Here, one must view the desired process both on the basis of its potential as a pollution abatement system and on the production of a marketable product. Due to the crude nature of the waste material, its fluctuating composition, and the volume of waste to be processed untreated or crude SCE would probably not serve as a suitable medium for the production of those products requiring more exacting fermentation techniques (i.e. antibiotics, vitamins, and other pharmaceutical preparations). On the other hand, the waste does appear suited to the production of crude enzyme preparations for industrial and domestic use, and in the production of SCP.

The major difficulty arising from the use of SCE as a fermentation substrate lies in the large volume of effluent to be processed. Prerequisites for the utilization of such volumes would include the selection of those species which possess very high growth rates and inhibit or reduce the growth of contaminating species present in waste water. From the standpoint of a microbiological utilization for SCE, a reduction in volume would be most desirable. Methods by which this may be accomplished are presently under consideration (F. G. Claggett personal communication). Preliminary data indicate that concentrated SCE does not exert any inhibitory effect on microbial growth or product formation.

Acknowledgments — The authors thank Mr J. Wong for assisting in the collection of the salmon-canning waste water.

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New Complexities in Zoogeography and Taxonomy of the Pygmy Whitefish (*Prosopium coulteri*)

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LINDSEY, C. C., AND W. G. FRANZIN. 1972. New complexities in zoogeography and taxonomy of the pygmy whitefish (*Prosopium coulteri*). J. Fish. Res. Bd. Canada 29: 1772–1775.

Pygmy whitefish (*Prosopium coulteri*) are recorded for the first time from the Peel–Mackenzie river drainage (Elliott Lake, Yukon Territory) and from the Hudson Bay drainage (Waterton Lakes, Alberta, in the South Saskatchewan–Nelson river system). The morphology of specimens from both localities contradicts the previously known pattern of a southeastern "low-rakered" and a northwestern "high-rakered" form (with the two forms occurring sympatrically in some lakes of the Bristol Bay area). Specimens from Elliott Lake, the most northerly known locality, resemble the southeastern form and those from Waterton Lakes the northwestern form. Both Waterton and Elliott lakes lie close to unglaciated refugia, suggesting that the species may have survived Wisconsin glaciation and diverged in several different watersheds.

LINDSEY, C. C., AND W. G. FRANZIN. 1972. New complexities in zoogeography and taxonomy of the pygmy whitefish (*Prosopium coulteri*). J. Fish. Res. Bd. Canada 29: 1772–1775.

Il s'agit de premières mentions du ménomini pygmée (*Prosopium coulteri*) dans le bassin Peel-Mackenzie (lac Elliott, Territoire du Yukon) et dans le bassin de la baie d'Hudson (lacs Waterton, Alberta, dans le régime des rivières Nelson et Saskatchewan-Sud). La morphologie des spécimens des deux endroits vient à l'encontre du concept établi d'une forme "à bas compte branchicténique" au sud-est et d'une forme "à haut compte branchicténique" au nord-ouest (les deux formes étant sympatriques dans certains lacs de la région de la baie de Bristol). Les spécimens du lac Elliott, l'endroit le plus au nord de leur aire de répartition connue, ressemblent à la forme du sud-est, alors que ceux des lacs Waterton se rapprochent de la forme du nord-est. Les lacs Elliott et Waterton sont situés à proximité de refuges qui n'ont pas été recouverts de glaciers. Il est donc possible que l'espèce ait survécu à la glaciation du Wisconsin pour se disperser ensuite dans plusieurs bassins hydrographiques différents.

Received June 29, 1972

THE pygmy whitefish *Prosopium coulteri* Eigenmann and Eigenmann, a distinctive large-scaled little fish confined to North America, has become an increasing puzzle to ichthyologists. Its known distribution is unique and highly disjunct: Pacific slope streams from Bristol Bay drainages south to the upper Columbia River; headwaters of the Yukon, Liard, and Peace rivers; and (separated by a gap of 1700 km) Lake Superior. Only a single species was thought to be involved (Eschmeyer and Bailey 1955) until McCart (1970) demonstrated that there are at least two forms within the "pygmy whitefish complex," two or even three occurring sympatrically in lakes near Bristol Bay. McCart suggested that each of the two forms may have spread postglacially from a distinct refugium within which it had diverged from its sibling.

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This note describes two recent collections of pygmy whitefish whose localities extend the known range into new drainages (the Peel–Mackenzie and the Saskatchewan–Nelson river systems) and whose morphology runs contrary to previously described geographic patterns of variation.

Sources of materials — On July 13, 1970, two specimens were taken by C. C. Lindsey and R. C. Manness from Elliott Lake, Yukon Territory (64°29′N, 135°35′W), 100 km north of Mayo (Fig. 1). Collection was by monofilament gillnet set on the bottom at a depth of 24 m. Other species collected in Elliott Lake and its tributaries were *Thymallus arcticus*, *Prosopium cylindraceum*, *Catostomus catostomus*, *Cottus cognatus*, *Salvelinus namaycush* and *Salvelinus alpinus*. (The two specimens of the latter species, although close to the known geographic range of *S. malma* and farther inland than previous records of *S. alpinus*, are tentatively identified as Arctic char on the basis of these counts following

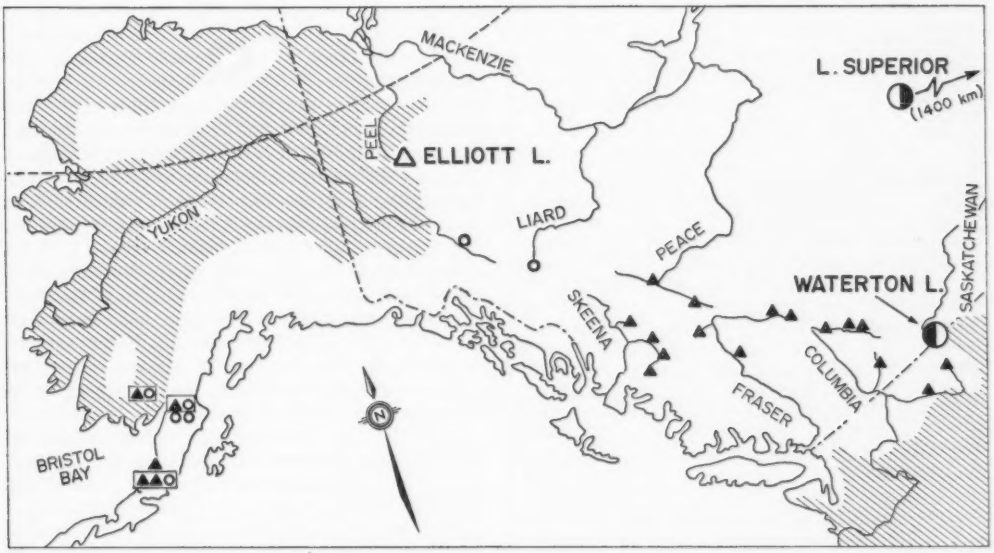

FIG. 1. Geographic distributions of forms of pygmy whitefish in western North America, modified from McCart (1970). Solid triangles are the "low-rakered" form (ratio: gillrakers/caudal peduncle scale rows < 0.95); open circles are "high-rakered" form (ratio: > 0.95). Rectangles enclose sympatric forms. Hatched areas unglaciated. All samples, except for Waterton and Elliott lakes, of five or more fish.

McPhail (1961): total gillrakers 23, 22; lower limb gillrakers 14, 13; lateral line pored scales 129, 131; pyloric caeca 31, 35; and vertebrae 68, 68.)

On August 10, 1971, two specimens were taken from Upper Waterton Lake, southwestern Alberta (Fig. 1), by W. G. Franzin and S. Franzin using monofilament gillnets set on the bottom at a depth of about 50 m off the mouth of Cameron Creek at Waterton Park townsite. At least 13 other species of fish have been recorded as probably native to Waterton Lakes.

We also have new records of pygmy whitefish in the Yukon River drainage from Quiet Lake, Yukon Territory (61°04′N, 133°04′W), Tatchun Lake, Yukon Territory (62°07′N, 136°07′W), and previously published records from Chadburn Lake, Yukon Territory, and Swan Lake, British Columbia (Teslin–Yukon system).

Morphology — The following counts (using the methods of McCart 1970) are given in the sequence of the two Elliott Lake specimens followed by the two Waterton Lakes specimens: Fork length (mm) 119.4, 111.9; 98.4, 88.0. Gillrakers 18, 16; 21, 20. Pored lateral line scales 53, 52; 52, 53. Horizontal scale rows around caudal peduncle 18, 18; 18, 18. Vertebrae 51, 51; 53, 54. Dorsal fin rays 12, 12; 12, 11. Anal fin rays 11, 12; 12, 13. Pectoral fin rays 15, 14; 14, 14.

Discussion — Previous collections of pygmy whitefish from western North America could be separated into two groups (Fig. 2) on the basis of dorsal fin ray counts and the ratio of gillrakers to caudal peduncle scales (McCart 1970). All southeastern collections (Peace, Skeena, Fraser and Columbia river drainages) fell in one group (McCart's "low-rakered" form); the second group, the "high-rakered" form, contained exclusively northwestern collections (Liard and Yukon rivers, and drainages in the Bristol Bay area). Three Bristol Bay collections contained two (or three) sympatric forms, one conforming to the northwestern group and one or two to the southeastern group. One Bristol Bay collection (Black Lake) fell exclusively in the southeastern group. Lake Superior specimens were intermediate between the two groups.

The striking geographic pattern in morphology suggested to McCart that the high-rakered form developed somewhere in the Yukon–Bering Sea area and the low-rakered form somewhere in the vicinity of the present Columbia Basin. According to this theory the low-rakered form subsequently spread north and west and has reached a few lakes in the Bristol Bay region where it occurs sympatrically with the high-rakered form. The fish in

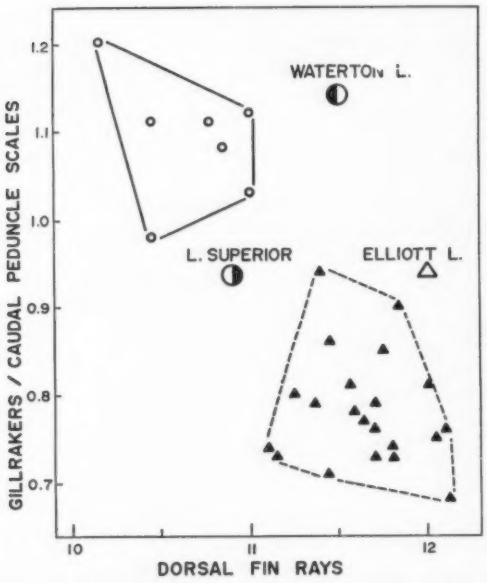

FIG. 2. Relation between population means of dorsal fin ray counts and ratio of number of gillrakers to that of caudal peduncle scales. Samples and symbols same as in Fig. 1. Solid line encloses all Liard and Yukon river samples plus high-rakered form from Bristol Bay area; broken line, all Peace, Skeena, Fraser, and Columbia river samples plus low-rakered Bristol Bay form.

Lake Superior presumably survived Wisconsin glaciation in a third refugium far to the east.

The morphology of specimens from both Elliott and Waterton lakes disrupts the pattern described. The very small sample sizes (2 for each lake, although all other points in Fig. 2 are each based on 5 or more fish) preclude detailed comparisons. Nevertheless, the Elliott Lake fish, although the most northerly of all collections (Fig. 1), clearly resemble the southeastern group in morphology (Fig. 2). Conversely, the Waterton Lakes fish, although geographically close to the southeastern group, lie morphologically remote from them.

The hypothesis that morphological variation has arisen during isolation in multiple refugia is not necessarily negated by the distinctive nature of these two new collections, provided it can be shown that Elliott and Waterton lakes might each have received fish from refugia other than the Columbia and Bristol Bay regions. To assess this possibility, the glacial history of each must be examined.

Elliott Lake lies close to the central and northern region of Yukon Territory which escaped glaciation (Fig. 1), but just inside the northwest margin of the area covered during the last glaciation by the Selwyn Lobe of the Cordilleran Ice Sheet. During the maximum ice advance, a long narrow glacier tongue projected northwest from the main ice mass to fill the valley now occupied by Elliott Lake and extend a further 33 km northwest downslope into the Hart River on the present Peel–Mackenzie river drainage (Hughes et al. 1969). During ice recession this tongue retreated upslope until it exposed the divide (between the Peel and Yukon river drainages) which at that time lay about 6.5 km northwest of the present Elliott Lake (Vernon and Hughes 1966, p. 14). As the ice face retracted still farther to the southeast, now receding downslope into the Yukon River basin, a proglacial lake was impounded between the ice front and the divide at an elevation of just below 1166 m. Meltwater discharging northward from this lake cut a channel through the old divide, thereby lowering the lake to somewhat above 1000 m and shifting the divide 11 km southeast to its present position south of Elliott Lake. The lake has apparently, since its inception, always had an outlet northwest into the Hart River. The proximity of Elliott Lake to an unglaciated refugium and the known sequence of events during ice retreat are consistent with the view that the somewhat distinctive Elliott Lake form of pygmy whitefish may have had its origin in a refugium within the Peel drainage basin.

Waterton Lakes, at an elevation of 1398 m, straddle the Alberta–Montana border just east of the continental divide (Fig. 1). The present lake basin was probably overrun by a tongue from the North Fork Belly Glacier of the Cordilleran ice complex (Alden 1932, pl. 37), but unglaciated terrain which harbored a series of shifting proglacial lakes evidently lay only a few kilometres to the east and south, although the details are obscure (Horberg 1954; Prest et al. 1968; Prest 1969). During early glacial retreat, the proglacial lake waters which filled the Waterton Valley probably escaped to the eastward and thence southward to the Missouri River system. Withdrawal of the Laurentide ice sheet eventually permitted establishment of the Saskatchewan–Nelson river system whereby Waterton Lakes now drain to Hudson Bay. There seems to be no evidence that Waterton Lakes ever had an outlet westward into the Columbia river system either during or after Wisconsin glaciation. In support of this contention, the nearest tributary of the Columbia, the North Flathead River, differs markedly in its fauna from that of Waterton Lakes. About eight fish species present in Waterton Lakes are absent from the North Fork Flathead River and four species present in the latter are absent from the former (Schultz 1941; Paetz and Nelson 1970; McAllister and Ward 1972). The crustacean

Mysis relicta is in Waterton but nowhere west of the continental divide; the amphipod *Pontoporeia affinis* is also in Waterton, and absent on the Pacific coast except for the single known occurrence in Lake Washington at Seattle (Ricker 1959). Segerstråle (1971) argued that the Lake Washington population probably reached there by crossing the continental divide from a Missouri River refugium. If this did occur (which presents some difficulties if only passive transport is envisaged), the route was presumably via the Fraser river system rather than the Columbia in order to place the amphipod in ice-dammed lakes in the Puget Sound region (Segerstråle 1971); hence, the crossover point of the continental divide would have been far to the north of Waterton. In summary, the proximity of Waterton Lakes to unglaciated regions in the headwaters of the Missouri River, the apparent absence of any water connection with the Pacific slope during or since Wisconsin glaciation, and the presence in Waterton of various other species of fish and crustaceans not found in the Columbia River system are all consistent with the view that Waterton Lakes pygmy whitefish differ morphologically from Pacific slope populations because they orginated from a different glacial refugium.

It may be argued that all the observed morphological variation represents recent adaptation to local environments and is without relevance to glacial history. However, fish from all the southeastern localities (except Waterton Lakes) are consistently different from most of those from the northwestern localities, even though both lake and stream collections are represented in both areas. The morphological characters used do not seem to be obviously correlated with local ecological conditions.

The available data suggest that pygmy whitefish survived the Wisconsin glaciation in several refugia, each containing one or more forms which possessed morphological distinctions either developed in situ or left over from earlier Pleistocene events. The following Wisconsin refugia might have been involved: (a) one in the Columbia River basin; (b) one close to Bristol Bay (which might have harboured two forms, one perhaps derived from a preWisconsin invasion from the south); (c) one in the upper Yukon River basin (which may or may not have been isolated from Bristol Bay watersheds); (d) one in the Peel River area (which is now tributary to the Mackenzie River but which during maximum glaciation was tributary to the Yukon River via the Porcupine (Hughes 1972)); (e) one in the Missouri River headwaters close to Waterton Lakes; and (f) one in the upper Mississippi River region which gave rise to the Lake Superior population. With all these possibilities for allopatric divergence, it is not remarkable that the present mosaic of characters is complex.

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Two New Host Species for the Parasitic Fungus *Ichthyophonus hoferi* in the Northwest Atlantic

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HENDRICKS, J. D. 1972. Two new host species for the parasitic fungus *Ichthyophonus hoferi* in the northwest Atlantic. J. Fish. Res. Bd. Canada 29: 1776–1777.

Microscopic examination of kidney tissues from eight Gulf of Maine fish species revealed cysts of the fungus *Ichthyophonus hoferi*, Plehn and Mulsow, in individuals from three species. Two of these species, the longhorn sculpin (*Myoxocephalus octodecemspinosus*) and the Atlantic cod (*Gadus morhua*), are new hosts for this parasite in Gulf of Maine waters. The other species, the yellowtail flounder (*Limanda ferruginea*), was previously reported as an *Ichthyophonus* host.

HENDRICKS, J. D. 1972. Two new host species for the parasitic fungus *Ichthyophonus hoferi* in the northwest Atlantic. J. Fish. Res. Bd. Canada 29: 1776–1777.

L'examen microscopique du tissu rénal de huit espèces de poissons du golfe du Maine révèle la présence de kystes du champignon *Ichthyophonus hoferi*, Plehn et Muslow, chez les individus de trois espèces. Deux de ces espèces, le chaboisseau à dix-huit épines (*Myoxocephalus octodecemspinosus*) et la morue franche (*Gadus morhua*), sont des hôtes nouveaux de ce parasite dans le golfe du Maine. L'autre espèce, la limande ferrugineuse (*Limanda ferruginea*), a déjà été signalée comme un des hôtes d'*Ichthyophonus*.

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THE parasitic fungus *Ichthyophonus hoferi* has been reported in North America from the sea herring, *Clupea harengus* (Cox 1916); the winter flounder, *Pseudopleuronectes americanus* (Ellis 1928); the alewife, *Alosa pseudoharengus* (Fish 1934); the rainbow trout, *Salmo gairdneri* (Rucker and Gustafson 1953); the yellowtail flounder, *Limanda ferruginea* (Powles et al. 1968); and numerous European marine and freshwater fishes (Reichenbach-Klinke 1954, 1956). This note reports this fungal parasite for the first time in longhorn sculpin (*Myoxocephalus octodecemspinosus*) and Atlantic cod (*Gadus morhua*) from northwest Atlantic waters. The Atlantic cod has been reported as an *I. hoferi* host in European waters (Lederer 1936), but not in North American waters.

The kidneys from 10 specimens of each of eight Gulf of Maine fish species were randomly collected for histological studies during spring 1971: longhorn sculpin (*M. octodecemspinosus*), Atlantic cod (*G. morhua*), yellowtail flounder (*L. ferruginea*), American plaice (*Hippoglossoides platessoides*), pollock (*Pollachius virens*), haddock (*Melanogrammus aeglefinus*), Atlantic argentine (*Argentina silus*), and Atlantic herring (*C. harengus harengus*). The longhorn sculpin were caught by bottom trawl from 91.5 m of water at 41°38.5′N, 55°18.5′W. The Atlantic cod were taken from two different stations: six from 256 m at 43°39′N, 63°50.5′W; and four from 104 m at 42°25.5′N, 65°30.5′W. Samples were fixed in Davidson's fixative, processed by routine methods, and stained with hematoxylin and eosin or Fuelgen picryl methyl blue triple stain (Farley 1969). One longhorn sculpin (28 cm fork length) and one Atlantic cod from each location (60 and 64 cm fork length) were infected. No gross lesions were detected in the three infected fish, and cysts were evident only in histological sections.

The fungal infection appeared to be in its early stages of development in all three fish, since relatively small areas of the kidneys were involved. Because samples were collected to study normal renal histology, no other tissues were collected from the infected fish. Therefore, the overall extent of the infection was not known. Only two of the several life history stages described by Sproston (1944) were found. Large, thick-walled, multinucleated plasmodia were most abundant (Fig. 1A, B, and 3A), but some plasmodia undergoing hyphal germination were also present (Fig. 2A, B). The host response of connective tissue proliferation was marked in most cases, forming heavily encapsulated cysts.

An advanced case of *I. hoferi* infection was found in one yellowtail flounder (approximately 37 cm fork length) taken from 93 m at 42°16′N, 70°31.5′W.

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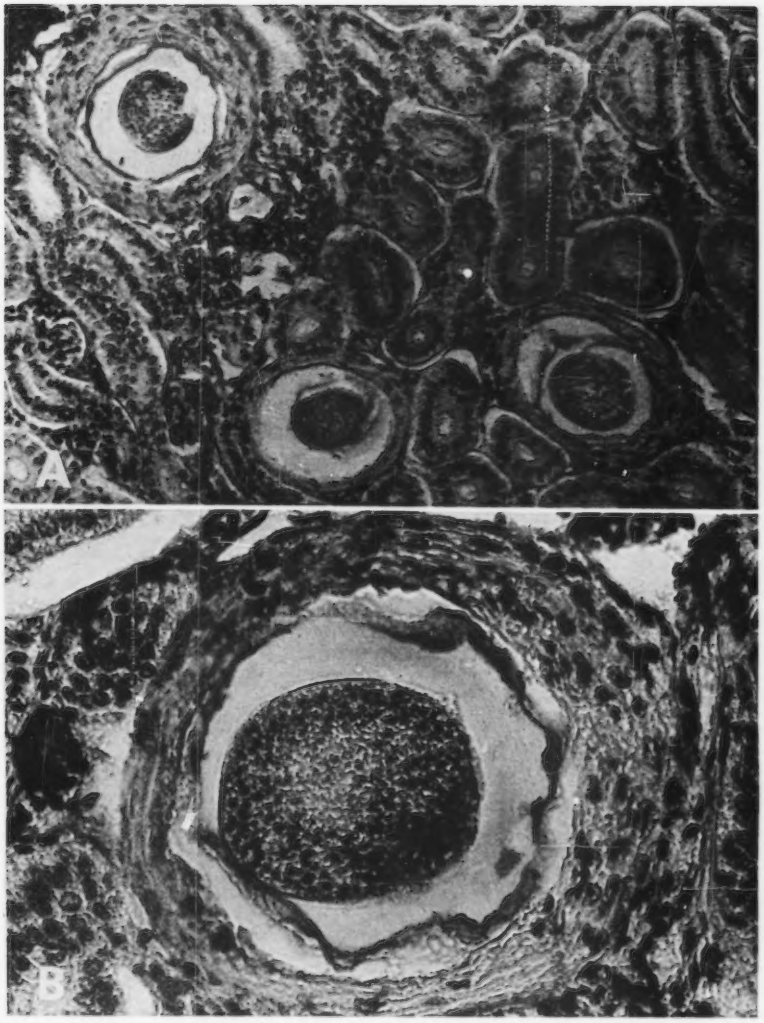

FIG. 1. Longhorn sculpin kidney. A, three (*Myoxocephalus octodecemspinosus*) resting cysts containing multinucleate plasmodia. Note pressure on kidney tubules and development of connective tissue. FPMB, ×240; B, resting cysts with a multinucleate plasmodium. FPMB, ×600.

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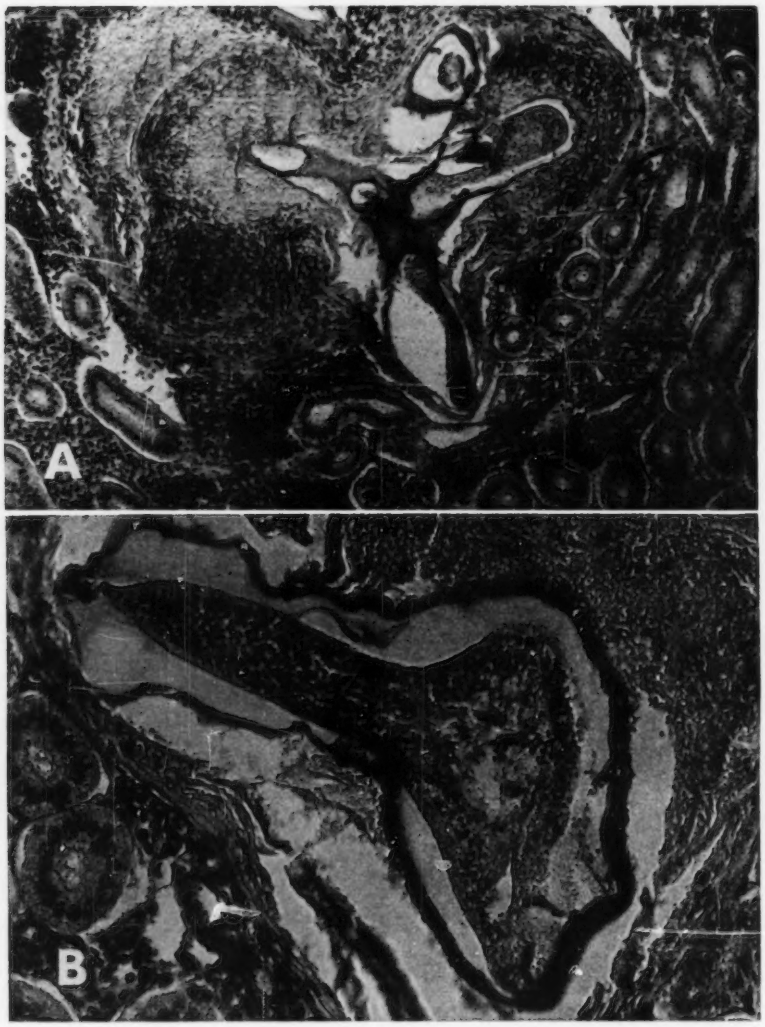

FIG. 2. Germination and hyphal development of fungal plasmodium in (*Myoxocephalus octodecemspinosus*) longhorn sculpin kidney. A, necrosis and connective tissue development. FPMB, ×150; B, heavy cyst wall, streaming of nuclei into the developing hypha, and connective tissue. FPMB, ×375.

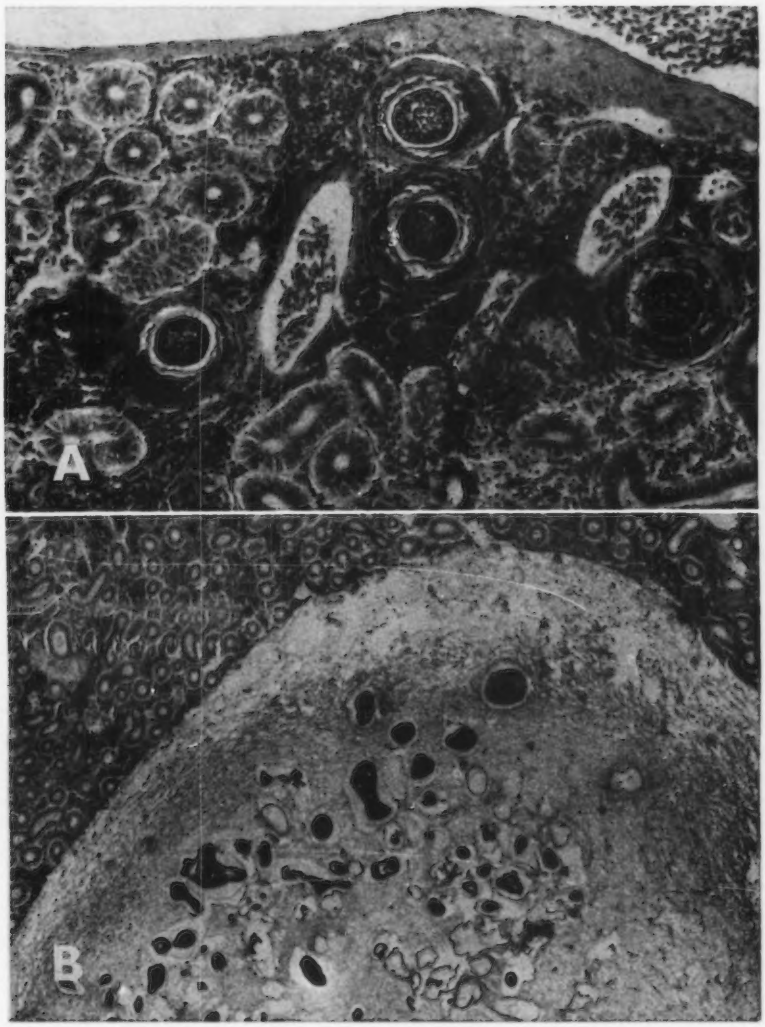

FIG. 3. *Ichthyophonus* cysts in A, Atlantic cod (*Gadus morhua*) kidney. FPMB, ×200; B, large lesion from yellowtail flounder (*Limanda ferruginea*) kidney. FPMB, ×50.

This lesion was grossly observable and had replaced much of the normal kidney tissue (Fig. 3B). Similar lesions in yellowtail flounder have been described by Powles et al. (1968) and Ruggieri et al. (1970). No other fish sampled had infections.

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Mercury Removal from Fish Protein Concentrate

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Regier, L. W. 1972. Mercury removal from fish protein concentrate. J. Fish. Res. Bd. Canada 29: 1777–1779.

The potential reclamation of mercury contaminated proteinaceous food by an extraction procedure such as employed in making fish protein concentrate was investigated. The addition of hydrochloric acid to the isopropanol extractant was found to give removals as high as 93% from dry swordfish protein concentrate. The normal Halifax isopropanol extraction process did not effect any significant removal of the mercury.

Preliminary studies of the variables indicated acid concentration, kind of alcohol (ethanol and isopropanol), alcohol concentration, extractant volume, and number of extractions were important in the extraction.

Regier, L. W. 1972. Mercury removal from fish protein concentrate. J. Fish. Res. Bd. Canada 29: 1777–1779.

L'auteur étudie la possibilité de récupérer les aliments du type protéique contaminés au mercure à l'aide d'un procédé d'extraction similaire à celui utilisé dans la fabrication des concentrés de protéines de poisson. L'addition d'acide chlorhydrique à l'extracteur isopropanol permet une récupération allant jusqu'à 93% à même le concentré de protéines de l'espadon. Le procédé d'Halifax d'extraction normale à l'isopropanol n'enlève pas de quantités significatives de mercure.

Une étude préliminaire des variables démontre que la teneur en acide, le genre d'alcool (éthanol ou isopropanol), la teneur en alcool, le volume d'extracteur et le nombre d'extractions jouent un rôle important dans l'extraction.

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THE recent recognition of the potential human health hazards from mercury as the result of eating fish with high residues of this element has presented a number of questions to the fishing industry. The development of sensitive and accurate methods of analysis has, of course, been the crucial factor in the definition of the scope and severity of the problems (Uthe et al. 1970).

It has been shown that the levels of mercury in freshwater fish of commercially significant species are related to their geographical area and the level of stream or lake contamination (Bligh 1972). Studies are in progress to define the extent and distribution of mercury contamination in salt-water species.

Most conventional food products made from fish contain muscle contaminants at the same level as the live animals. Thus, the raw fish must have less than the official action or tolerance level. However, when considering a product such as fish protein concentrate (FPC) in which the components of the fish are fractionated, we are presented with an opportunity to try to remove most of a contaminant such as mercury. Also, if an FPC industry is to develop, there must be data to show whether the processes used increase or decrease the potential hazard from mercury in fish.

The preliminary work reported here was undertaken to show whether the FPC process removes mercury and to try to enhance the removal of the element from the FPC.

Materials and methods — The raw material used for this investigation was swordfish (*Xiphias gladius*) which had been caught commercially and was being retained due to high levels of mercury. The frozen fish, which weighed about 45 kg each with head and tail removed, were cut on a meat saw to remove the backbone and then into about 2¼-kg pieces. The pieces were thawed in air at room temperature, chopped in a Fitzmill with a Guilocutter blade, and deboned in a Yanagiya Deboner with 4-mm perforations in the separator drum.

A portion of the deboned meat was refrozen in polyethylene bags and kept at −18 C. The remainder of the meat was used to make FPC in the pilot plant by the Halifax Isopropanol (IPA) extraction method (Power 1962). Samples were taken of the filter cake after each of the three extractions and of the product after drying. These samples, together with a sample of the deboned meat, were analyzed for mercury by the atomic absorption method (Uthe et al. 1970).

The analytical results of these samples are shown in Table 1. The extraction method apparently does not remove any significant amount of the mercury. The apparent concentrating effect here, which is noted when the results are reported on a dry weight basis, is the result of the extraction process. The lipids and most of the water soluble or lower molecular weight compounds are removed in the extraction leaving a residue which is practically all protein. Although the extraction is made under slightly acid conditions (*p*H 5.5), the theoretical binding of the mercury to the protein is confirmed.

Since the normal process did not remove the mercury, a more severe system for extraction was tried. The completed swordfish FPC was re-extracted with alcohol

TABLE 1. Mercury content of swordfish meat and fish protein concentrate (FPC).

Sample	Hg ppm wet basis	% dry material	Hg ppm dry basis
Deboned swordfish	1.01	32.4	3.12
Filter cake			
First extracted FPC	2.20	46.7	4.71
Second " "	3.05	54.6	5.59
Third " "	3.16	53.8	5.88
Finished FPC	5.69	97.8	5.82

TABLE 2. Mercury removal from swordfish FPC by alcohol acidified with hydrochloric acid.

Alcohol	% HCl added	Hg ppm dry basis	% removed
99% Isopropanol	0.55	6.3	0
"	1.09	4.3	32
"	1.61	3.0	52
"	2.61	1.5	76
"	4.43	0.92	86
70% Isopropanol	2.61	2.8	57
95% Ethanol	0.28	6.5	0
"	0.55	6.2	0
"	1.09	6.3	0
"	2.61	1.7	74

TABLE 3. Mercury removal from swordfish FPC under several conditions of extraction number, volume, and contact time.

No. of extraction	Solvent volume (*ml*)	Extraction time (*min*)	Hg ppm dry basis	% removal
1	100	15	2.5	60.3
1	200	15	1.2	81
1	400	15	1.2	81
2	100	15	1.2	81
3	100	15	0.78	87.6
4	100	15	0.43	93.1
2	100	5	1.7	73
2	100	45	0.92	85.3

acidified with hydrochloric acid at several concentrations in the laboratory. A 25-g portion of the FPC was mixed with 100 ml of the acidified alcohol and allowed to stand for 15 min at room temperature. The thick slurry was then filtered through a sintered glass funnel, resuspended in 75 ml of the acidified alcohol for 5 min, and refiltered. The filter cake was washed with four 50 ml portions of the alcohol (which did not contain added acid) and dried overnight in a vacuum oven at 50 C. The extracting solution, compositions, and the mercury residue in the samples are shown in Table 2. The difference between the mercury level in the regular FPC samples in Table 1 and Table 2 is due to analyses in different laboratories (Zitko et al. 1971).

Results and discussion — In the presence of hydrochloric acid the isopropanol was a more effective extracting agent than the 70% isopropanol or the 95% ethanol. With equivalent added hydrochloric acid concentrations the 70% isopropanol removed only 57% of the mercury while the 99% isopropanol removed 76%. The alcohol concentrations noted are not exact, due to the water in the 37% hydrochloric acid solution added to give the tabulated levels of acid concentration.

The samples extracted with 95% ethanol and 70% isopropanol showed significant darkening on drying while those extracted with the 99% isopropanol all retained the same light tan color of the starting material. The darkening is taken as an indication of some protein degradation.

A series of samples were extracted with isopropanol acidified with glacial acetic acid concentrations of 0.4, 1.2, 3.6, and 10.8%. None of these samples showed any mercury removal.

The effects of numbers of extractions, extraction times, and liquid–solid ratio were also subjected to preliminary investigation. In these extractions, the solvent used was 2.6% hydrochloric acid in isopropanol and the usual ratio was 100 ml solvent to 25 g of the swordfish FPC. Each one of the samples was rinsed with four 50-ml portions of 99% isopropanol. The results are shown in Table 3.

With extraction times of 15 min, samples with 1, 2, 3, and 4 extractions showed removals of 60.3, 81, 87.6, and 93.1% of the mercury, respectively. These results indicate the need for a multiple batch or continuous counter current system to remove the contaminant. However, when single extractions of 15 min each were made using solvent volumes of 100, 200, and 400 ml per 25-g sample, the mercury removals were 60.3, 81, and 81%; which indicated some value in increasing the extracting solvent volume. Finally, using double extractions with 100-ml solvent for periods of 5, 15, and 45 min gave removals of 73, 81, and 85.3%. The time of contact thus has a significant effect also and must be considered if one is to try to optimize the removal of mercury from FPC.

Conclusions — These preliminary experiments show that nearly all the mercury can be removed from swordfish FPC under conditions which should not cause any significant harm to the nutritional value of the protein, using a solvent which will not introduce any significant toxicity questions. If the sample which was extracted for 15 min with 200 ml of 2.6% hydrochloric acid in isopropanol is taken as an example, a removal of 81% of the mercury was found. This is a decrease from 6.3 ppm to 1.2 ppm in the dry FPC. If this product were used in a food with a moisture content of 75%, the level of mercury would be 0.3 ppm which is well below the 0.5 ppm regulatory action level.

Acknowledgments — The assistance of R. Legendre in producing the FPC in the pilot plant is gratefully noted. The mercury analyses were done through the cooperation and supervision of F. A. J. Armstrong at the Freshwater Institute, Fisheries Research Board, Winnipeg, Man., and D. C. Horne, Fish Inspection Laboratory, Halifax, N. S. The comments and support of V. Zitko, Biological Station, Fisheries Research Board, St. Andrews, N.B., were helpful in starting this study.

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Some Physiological Consequences of Handling Stress in the Juvenile Coho Salmon (*Oncorhynchus kisutch*) and Steelhead Trout (*Salmo gairdneri*)

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WEDEMEYER, G. 1972. Some physiological consequences of handling stress in the juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). J. Fish. Res. Bd. Canada 29: 1780–1783.

The stress of handling juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*) in soft water and in water with added salts was evaluated using blood and tissue chemistry fluctuations as indices of metabolic and endocrine function. Changes in plasma glucose, chloride, calcium, and cholesterol levels indicated that significant osmoregulatory and metabolic dysfunctions can occur and persist for about 24 hr after handling in soft water. Pituitary activation, as judged by lack of interrenal ascorbate depletion, did not occur. Increasing the ambient NaCl and Ca^{++} levels to about 100 milliosmols and 75–120 ppm, respectively, partially or completely alleviated the hyperglycemia and hypochloremia indicating that the stress of handling had been reduced.

WEDEMEYER, G. 1972. Some physiological consequences of handling stress in the juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). J. Fish. Res. Bd. Canada 29: 1780–1783.

L'auteur évalue le stress causé par la manipulation chez les jeunes saumons coho (*Oncorhynchus kisutch*) et truites arc-en-ciel (*Salmo gairdneri*) dans de l'eau douce et dans de l'eau à laquelle des sels ont été ajoutés. Les fluctuations dans la chimie du sang et des tissus ont servi d'indices des fonctions métaboliques et endocrines. Des changements de teneur en glucose, chlorures, calcium, et cholestérol dans le plasma sont le signe de sérieuses malfonctions osmorégulatrices et métaboliques, qui peuvent persister jusqu'à environ 24 h après manipulation en eau douce. L'hypophyse n'est pas stimulée, à en juger par l'absence de déplétion d'acide ascorbique surrénalien. Une augmentation du NaCl et du Ca^{++} ambiants aux niveaux d'environ 100 milliosmols et 75–120 ppm, respectivement, allège partiellement ou complètement l'hyperglycémie et l'hypochlorémie, signe d'une diminution du stress manipulatoire.

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HANDLING stress is an inescapable part of the life of hatchery fishes, whether it occurs during cultural operations or during experimental work in laboratories. If the stress is relatively severe, immediate or delayed mortalities ("hauling" or "handling" loss) can follow and disease epizootics, particularly those due to faculative pathogens, can occur (Horton 1956; Collins and Hulsey 1963; Wedemeyer 1970; Lewis 1971). These undesirable effects are presumably due to a complex of factors centering around activation of the pituitary–interrenal axis together with osmoregulatory dysfunction (Podoliak 1967; Lewis 1971). As one example, handling stress-induced interrenal stimulation has been observed in several of the salmonid fishes (Fagerlund 1967; Wedemeyer 1969).

There are, however, many instances in which the physiological consequences of handling are not as immediately obvious. There may be few behavioral changes after handling, and thus little visible evidence that stress has even occurred. Accordingly, in the absence of actual death as an indicator, the severity of handling stress and the length of time a fish needs for recovery are frequently unclear.

To help resolve this problem, a series of experiments was performed to measure some of the blood chemistry imbalances accompanying a relatively mild, standardized, handling stress and to estimate the time needed for recovery using soft water and water with salt additions. The juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*) were chosen as test species.

Materials and methods — Juvenile, hatchery-reared fish, 10–15 cm long, were acclimated to the laboratory for several months in 10 C water of 20 ppm total hardness containing about 3 ppm Cl^- and 5 ppm Ca^{++}; *p*H 6.8. They were maintained on the Abernathy dry diet

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(Fowler and Burrows 1970), but fasted overnight before blood sampling and during the experimental period.

The total handling stress consisted of netting out a 10-fish subsample, to determine basal values, and then simply transferring an additional lot of 40 fish, in about 10 liters of water, to other aquaria about 25 m away. Subsequent 10-fish subsamples were taken at 1, 3, 5, and 24 hr. Netting activity was as gentle as practicable to minimize the stress of sampling.

General sampling techniques, anesthesia and interrenal ascorbate, blood glucose, cholesterol, chloride, and calcium analyses were as previously described using individual fish (Wedemeyer and Chatterton 1971).

For the experimental work on the effect of salt additions, the fish were transferred into water containing either 100–250 milliosmols NaCl or 75–120 ppm Ca^{++} (as $CaSO_4$); a situation analogous to stocking hatchery fish in waters of differing chemistry.

Results and discussion—When juvenile coho salmon and steelhead trout were given the mild handling stress described, several blood chemistry imbalances immediately occurred and persisted for as long as 24 hr before a measure of homeostasis was regained.

In both species, a statistically significant ($P = 0.05$) hyperglycemia occurred after the fish were handled. Blood glucose levels increased by a factor of 3–4 during the first hour after handling and remained high for at least 5 hr. Maximum hyperglycemia occurred about 3 hr after handling but, by 24 hr, homeostasis had been re-established in both fishes and the blood sugar levels had declined to approximately initial values (Fig. 1A).

The response of plasma cholesterol to stress in these two fishes paralleled a behavioral change

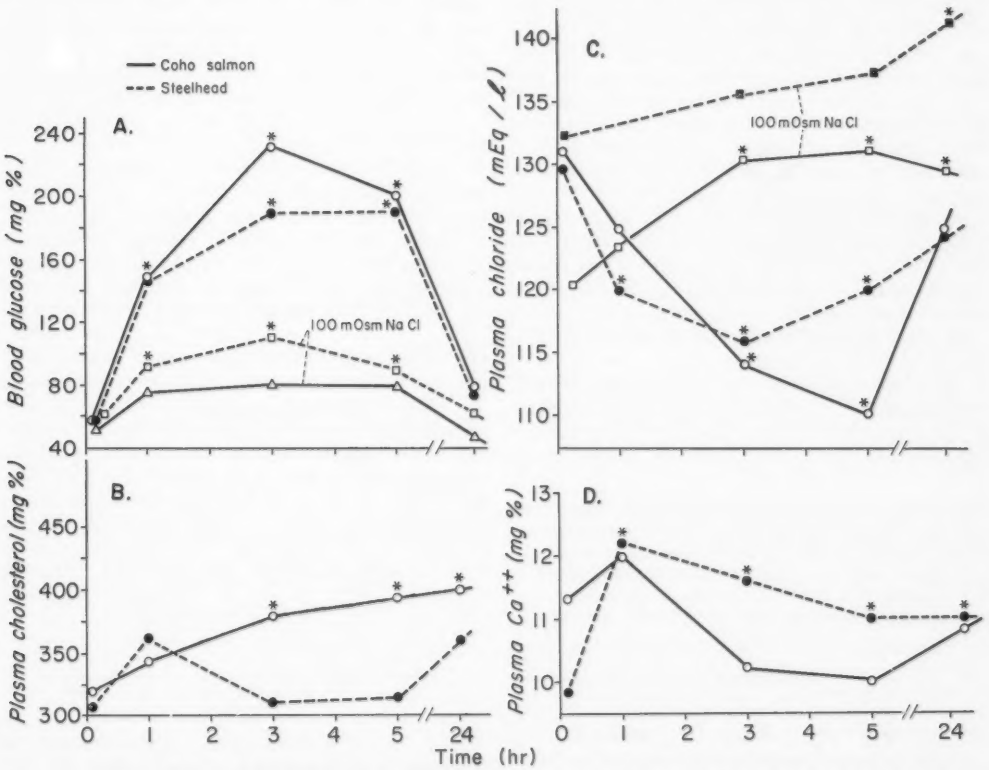

FIG. 1. A, Hyperglycemia in the steelhead trout (*Salmo gairdneri*) and coho salmon (*Oncorhynchus kisutch*) following handling. Upper curves, no salt additions; lower curve, 100 milliosmols NaCl (0.3%) added; B, Progressive hypercholesterolemia in the coho salmon following handling. There was no significant change ($P = 0.05$) in the steelhead trout; C, Lower curves: hypochloremia (osmoregulatory dysfunction) and recovery in the steelhead trout and coho salmon following handling. Upper curves, inhibition of chloride depletion following handling in the presence of 100 milliosmols NaCl; D, Plasma Ca^{++} levels following handling in the coho salmon and steelhead trout.

frequently noted in this laboratory. In the coho, which normally refuse to feed for a time following this type of handling, a mild, but sustained, hypercholesterolemia developed which did not occur in the steelhead (Fig. 1B). Since adrenal hydrolysis of serum cholesterol esters may be responsible for stress-induced hypercholesterolemia, it is reasonable that the fright response could influence the amount of free cholesterol produced during handling.

Significantly, interrenal vitamin C depletion, which is usually taken as an index of adrenocorticotrophin production, did not occur in either species (Table 1). Thus, plasma cortisol determinations were considered unnecessary. Evidently, the mild handling stress involved in the present study was not severe enough to cause any substantial activation of the pituitary–interrenal axis.

Determinations of plasma Cl^- and Ca^{++} following handling showed that blood levels of both ions fluctuated, an indication of osmoregulatory dysfunction. Plasma Cl^- levels fell steadily for several hours in both species and then began to rise with complete recovery within about 24 hr (Fig. 1C, lower two curves). These changes are probably blood electrolyte reflections of both chloride cell dysfunction and laboratory diuresis; however, the scope of this study did not extend to urinalysis.

Blood Ca^{++} responded somewhat differently to handling stress than did Cl^- (Fig. 1D). The plasma Ca^{++} fluctuations in the coho were not statistically significant but, in the steelhead, an initial hypercalcemia occurred which was sustained and blood calcium levels were still significantly ($P = 0.05$) elevated 24 hr following handling.

Since experience has shown that "hauling loss" can sometimes be reduced by salt (NaCl) additions (Collins and Hulsey 1963; Lewis 1971), the effect of supplemental NaCl and $CaSO_4$ on certain of the blood chemistry imbalances due to handling was studied. It has been suggested that loss of blood electrolytes may be partly responsible for the delayed mortality sometimes caused by stress (Podoliak 1967).

As shown in Fig. 1C, adding 0.3% (about 100 milliosmolar) NaCl to the water prior to handling prevented the usual hypochloremia in both species. Apparently, osmoregulation was then sufficiently facilitated that plasma Cl^- levels could be maintained during stress. Actually, some hyperchloremia occurred which, though statistically significant ($P = 0.05$), probably would not be of much biological consequence. Higher NaCl levels, up to isotonicity (235 milliosmols), were also tested but were not substantially better than 100 milliosmols. NaCl solutions of osmolality approaching that of blood are usually detrimental to freshwater fishes (Lewis 1971).

TABLE 1: Interrenal vitamin C in the juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*) following handling. There was no significant depletion in either species ($P = 0.05$). Each value is the mean ± standard deviation for an eight-fish sample.

Time (*hr*)	Interrenal ascorbate (*μg/g tissue*)	
	Coho	Steelhead
0	339±70	267±51
1	353±39	280±49
3	341±65	285±24
5	346±77	279±46
24	390±47	313±21

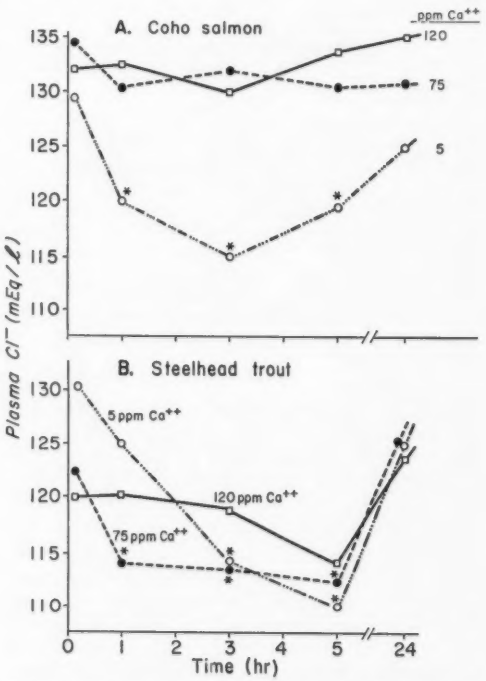

FIG. 2. A, The amelioration of handling-induced osmoregulatory dysfunction (hypochloremia) by Ca^{++} additions to the water, in juvenile coho salmon (*Oncorhynchus kisutch*); B, Effect of Ca^{++} additions on osmoregulatory dysfunction (hypochloremia) in the juvenile steelhead trout (*Salmo gairdneri*).

*indicates significantly different from "0" hour controls ($P = 0.05$).

Since hypochloremia is one indication of incipient osmoregulatory dysfunction, the present data on Plasma chloride fluctuations may help explain previous empirical findings on the use of salt to reduce "hauling loss" mortality (Collins and Hulsey 1963).

Significantly, NaCl additions also tended to reduce handling-induced hyperglycemia in these two species (Fig. 1, lower curves). Again, 100 milliosmols NaCl was sufficient.

To evaluate the role of Ca^{++} in alleviating handling stress, the normal 5 ppm Ca^{++} in the water supply was supplemented with sufficient $CaSO_4$ to bring the total Ca^{++} levels up to 75 or 120 ppm. This amount of $CaSO_4$ had no effect on the *p*H.

As seen in Fig. 2A, increasing the environmental Ca^{++} to 75 ppm, or more, completely prevented the usual stress-induced hypochloremia in juvenile coho. In contrast, Cl^- regulation in the steelhead did not benefit as much from Ca^{++} additions, though there was some improvement at 120 ppm (Fig. 2B). Similarly, supplemental Ca^{++} (or NaCl) was found to have little effect on the mild handling-induced hypercholesterolemia which normally developed in the coho.

Plasma Ca^{++} levels in the coho, following handling, were somewhat elevated by the addition of 75 or 120 ppm Ca^{++} to the water which, in turn, effectively prevented the mild (nonsignificant) hypocalcemia which otherwise occurred (Fig. 1D). Plasma Ca^{++} levels did not drop in the steelhead following handling, so the effect of supplemental calcium in the water on plasma Ca^{++} was not investigated.

In summary, even relatively mild handling in soft water imposes a stress of some magnitude on the homeostatic mechanisms of the juvenile coho salmon and steelhead trout. Due to the sublethal stress occurring in this study, survival of the handling was assured but normalization of metabolic and osmoregulatory function required up to 24 hr. Increasing the ambient NaCl level to about 100 milliosmols (0.3%) and the Ca^{++} content to 75 or 120 ppm partially or completely alleviated some of the metabolic and osmoregulatory fluctuations (hyperglycemia and hypochloremia) caused by handling. Thus, these results help to explain past empirical findings that salt additions can reduce the "hauling loss" mortality of certain species.

Further research into the metabolic effects of sublethal handling (and other) stress should be helpful in defining the water quality and cultural conditions required for optimum fish health.

Acknowledgments—The technical assistance of N. E. Buroker contributed greatly to the success of this study.

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Device for Measuring Length and Girth of Fish[1]

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HUNTER, C. J., AND C. O. WHEELER. 1972. Device for measuring length and girth of fish. J. Fish. Res. Bd. Canada 29: 1784–1785.

Continued improvement in fish-measuring devices is necessary in fishery science. A length and girth measuring device was developed that will make multiple measurements rapidly on live fish with accuracies to 1 mm. Construction plans are available.

HUNTER, C. J., AND C. O. WHEELER. 1972. Device for measuring length and girth of fish. J. Fish. Res. Bd. Canada 29: 1784–1785.

En biologie des pêches, on doit sans cesse améliorer les appareils de mesure des poissons. Nous avons mis au point un appareil pouvant effectuer rapidement sur des poissons vivants de multiples mesures de longueur et de circonférence, précises au millimètre près. Les intéressés peuvent se procurer les plans de cet appareil.

Received July 4, 1972

THE accuracy of fish measurements has been a historical problem in fishery science. Girth measurements are especially important in gillnet fisheries for defining the fish size–mesh size relation. The sizes and shapes of target fishes are important in many fishing gear studies (e.g. Templeman 1963; Hodder and May 1965; Regier and Robson 1966; Shestov 1966; and Swartz and van Engel 1968), making it necessary to use a device which accurately and rapidly measures length and girth. Two girthometers have been described in the literature (Berst and McCrimmon 1961; Wydoski and Wolfert 1968). Both machines used the same principle (constant tension) for measuring the girth, but the one by Wydoski and Wolfert was more refined and was equipped with a length-measuring scale.

While conducting a gillnet study on sockeye salmon (*Oncorhynchus nerka*) during 1968–70, a measuring device was required that would make multiple girth and length measurements accurately and quickly on live but narcotized fish. The above described machines were limited in measuring live fish rapidly. An improved length and girth measuring device (Fig. 1) was developed with the help of our engineering and design staff. It consisted of a shallow, stainless steel, U-shaped cradle with a scale of 0.5-cm divisions engraved on the bottom. This scale was used to measure fork lengths up to 89 cm. A sliding pointer, mounted on one side with another metric scale, was used to measure lengths from the tip of the fish's snout to intermediate points on the body. A .0625-inch (1.5875-mm) stainless steel cable passed through a slot in the cradle (Fig. 1) to form a loop in which the fish was placed. One end of this cable was secured to another pointer moving along a metric scale; when the loop was tightened around the body of the fish, the girth was indicated by the sliding pointer. The loop became larger or smaller by moving the pointer in the appropriate direction. Girths up to 47 cm could be thus measured. In the process of measuring live fish, especially in an experiment in which the results may be affected by physical stress, the amount of handling and the time the fish is out of water are very important. In this particular study, there was concern about the degree of stress placed on each fish since fish survival was the principal criterion in the study. Therefore, to increase the measuring speed, accuracy was limited to the nearest 5 mm. Measurements to the nearest 5 mm were considered adequate for both length and girth of mature sockeye salmon (these fish averaged about 300 mm for dorsal girth and 600 mm for fork length). This device, however (with a 1.0-mm scale), is capable of 1.0-mm accuracy. Seven measurements (Fig. 2) required between 20 and 30 sec/fish. A three-man team was employed — one to hold the fish, one to make and call out the measurements, and the third to record the data.

Accuracy to 1.0 mm was obtained on trial measurements of rigid cylinders of 161–335-mm circumference. Comparative measurements of sockeye salmon were made with a metric tape. Of 100 comparisons, 39 measured the same, 43 had a difference of 5 mm, 17 had a difference of 10 mm, and 1 differed by 15 mm. This measuring device

[1]Detailed construction plans are available upon request from the authors at the Northwest Fisheries Center, National Marine Fisheries Service, 2725 Montlake Blvd. E., Seattle, Wash. 98112.

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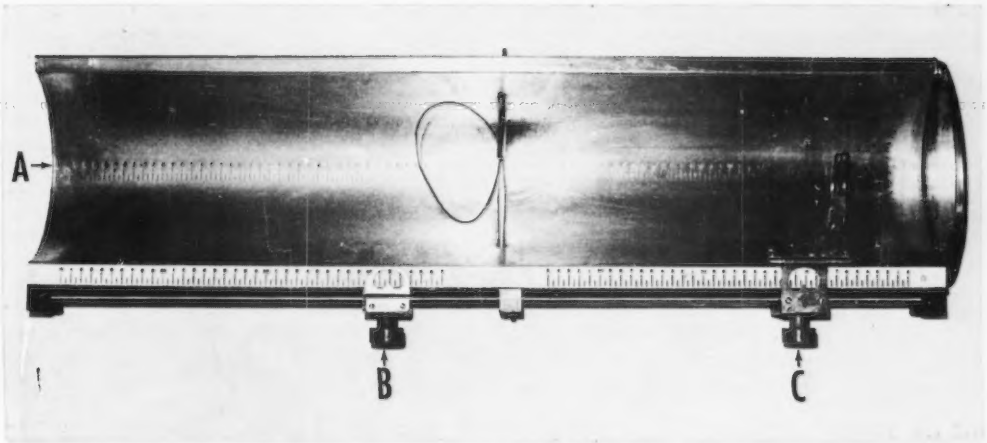

FIG. 1. Fish length and girth measuring device: A, fork length scale; B, girth scale; C, intermediate length scale.

Hunter and Wheeler — J. Fish. Res. Bd. Canada

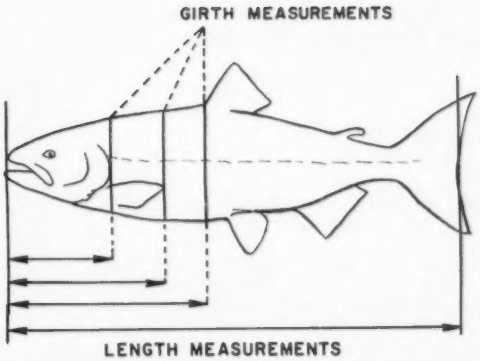

FIG. 2. Location of length and girth measurements recorded for each specimen.

recorded the same or smaller measurements in all cases except 12 which measured 5 mm larger. Replicate length and girth measurements at various body marks of six fish were not more than 5 mm different. However, because the measurement was interpolated to the nearest whole or half centimeter mark, the actual error was probably less than 2.5 mm. Only 18% of girth and 17% of length replicate measurements differed. This device, built to withstand severe corrosive conditions, can be used to measure lengths and girths with considerable speed and consistency. It is capable of a wide range of measurements on both live and dead fish.

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The Representation of Lower Molecular Weight Fatty Acids by the Bligh and Dyer Extraction Method

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HURST, R. E. 1972. The representation of lower molecular weight fatty acids by the Bligh and Dyer extraction method. J. Fish. Res. Bd. Canada 29: 1786–1787.

The Bligh and Dyer method of lipid extraction was investigated to determine the distribution of low molecular weight free fatty acids in the organic phase. Two solvent systems were studied: one using chloroform, methanol, and distilled water; the other using an aqueous fish extract containing natural buffer in place of distilled water. The low molecular weight fatty acids were not well represented in the chloroform layer and the presence of a buffer further depressed their distribution into the organic phase. Proportionately with increased molecular weight a greater percent of acid was recovered in the chloroform. Essentially total partitioning into the organic phase in both systems occurred at a carbon chain length of ten (decanoic acid).

HURST, R. E. 1972. The representation of lower molecular weight fatty acids by the Bligh and Dyer extraction method. J. Fish. Res. Bd. Canada 29: 1786–1787.

Nous évaluons les propriétés de la méthode d'extraction des lipides de Bligh et Dyer pour l'étude de la répartition des acides gras libres de faible poids moléculaire dans la phase organique. Deux systèmes de solvants ont été choisis, l'un comprenant du chloroforme, du méthanol, et de l'eau distillée, et l'autre un extrait aqueux de poisson contenant un tampon naturel au lieu de l'eau distillée. Les acides gras à faible poids moléculaire ne sont pas très bien représentés dans la couche de chloroforme, et la présence d'un tampon diminue davantage leur distribution dans la phase organique. Le pourcentage d'acide récupéré dans le chloroforme augmente en proportion directe du poids moléculaire. Un partage pratiquement total dans la phase organique des deux systèmes se produit à une longueur de chaîne de carbone de dix (acide décanoïque).

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WHEN the Bligh and Dyer (1959) procedure is employed to isolate lipids in which free fatty acids are to be measured; for example, during fish storage experiments, the lower molecular weight acids will not be quantitatively partitioned into the chloroform layer (Bowman and Beroza 1966; Schmid and Hunter 1971). In order to determine the distribution of short chain fatty acids between the two phases, an aqueous fish extract containing natural buffer was incorporated into the system. Further, the point within the homologous series at which quantitative recovery in the organic phase occurs was determined.

Materials and methods — Standard .2-N solutions of straight chain fatty acids ranging from formic to lauric acid in chain length were prepared. Two solvent systems were used, one of chloroform methanol and distilled water as a nonbuffered system and one of chloroform, methanol, and aqueous extract of fish muscle which contained natural buffer. The solvents were mixed in the proportions of 1:2:0:8, respectively, to give a single phase. The fish muscle extract was exhaustively extracted with chloroform to ensure removal of essentially all residual fatty acids. To a separatory funnel containing 38 ml of the mixed solvents, 2 ml of standard fatty acid solution was introduced; chloroform and water were then added to make the proportions 2:2:1.8 to create a two phase system. Both phases of the model system and the chloroform phase of the buffer system were titrated with .04-N KOH using bromothymol blue as an indicator. Methanol and water were added to the chloroform phase to ensure a satisfactory endpoint.

Results and discussion — Formic and acetic acids added to the nonbuffered system were partitioned to the extent of 14 and 20% in the organic phase (Fig. 1). These recoveries were depressed to 3% for both acids in the buffered system. As molecular weight increased in the homologous series of acids, there was a proportionately greater percent distribution into the chloroform. Decanoic acid and the fatty acids with chain lengths greater than ten carbons were quantitatively recovered in the organic phase of both systems.

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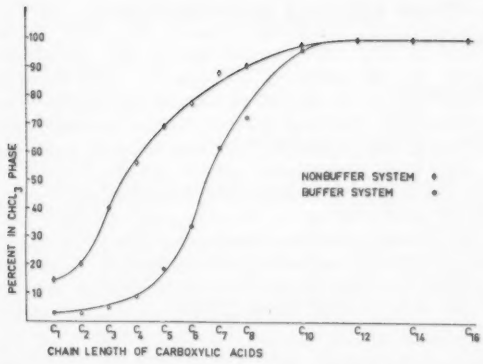

FIG. 1. Distribution of fatty acids in chloroform phase.

Accumulation of free fatty acids has been widely used as an index of lipid deterioration in fish (Sigurdsson 1947; Hillig et al. 1958; Hughes 1960). The increase of long chain fatty acids during processes such as cold storage can be mainly attributed to the hydrolysis of triglycerides or phospho-lipids (Banks 1967) while an increase in short chain acids can occur as products of autoxidation (Keeney 1962) or from the reduction of trimethylamine oxide through bacterial action (Watson 1938).

As over 90% of the fatty acids associated with the lipids of commercially important fish have a chain length of fourteen carbons or greater (Ackman 1967), this percent of the total free fatty acids derived from hydrolysis would be extracted quantitatively by the method of Bligh and Dyer. Short chain fatty acids, however, accumulating from autoxidation or bacterial reduction, will be ineffectively partitioned in the chloroform phase.

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World Distribution of Rainbow Trout (*Salmo gairdneri*): Further Observations

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MACCRIMMON, H. R. 1972. World distribution of rainbow trout (*Salmo gairdneri*): further observations. J. Fish. Res. Bd. Canada 29: 1788–1791.

This note supplements a previous paper on the world distribution of the rainbow trout (*Salmo gairdneri*). While strong public acceptance of the species as a sport and food fish is expected to intensify the propagation and use of wild and domestic strains, no significant extension in naturalized range is anticipated because of environmental limitations.

MACCRIMMON, H. R. 1972. World distribution of rainbow trout (*Salmo gairdneri*): further observations. J. Fish. Res. Bd. Canada 29: 1788–1791.

Cette note fait suite à une publication antérieure sur la répartition mondiale de la truite arc-en-ciel (*Salmo gairdneri*). La grande popularité de cette espèce comme poisson de sport et comme aliment contribuera sans doute à intensifier la propagation de lignées sauvages aussi bien que domestiques. Cependant, considérant les contraintes écologiques, nous ne prévoyons pas d'extension significative de l'aire de répartition naturelle de l'espèce.

Received August 18, 1972

THIS note supplements the previous account (MacCrimmon 1971) on the present world distribution of the rainbow trout (*Salmo gairdneri*). Modifications and additions are largely the result of personal communications arising from the original paper. The author expresses his appreciation to the many correspondents who have confirmed the stated distribution or have provided more precise details on local fisheries which have made this supplemental note possible.

In the original paper the endemic range shown included that of the California golden trout (*Salmo aquabonita*) and gila trout (*Salmo gilae*), both forms being recognized as distinct species in the American Fisheries Society checklist (Bailey 1960). The reader should refer to Fig. 1 in that paper for the native geographical ranges of the various species and subspecies of the rainbow and golden trout series.

Introductions and Naturalized Distribution

AFRICA

Swaziland — Although attempted rainbow trout introductions were not reported for Swaziland in the original paper, fish generally assumed to be rainbow trout were introduced there in 1908 under the auspices of the Transvaal Fisheries (Clay MS 1972). About 40,000 trout, including some brown trout (*Salmo trutta*), were planted between 1908 and 1930, but no self-sustaining populations resulted. At least some of the eggs came from the Stellenbosch Hatchery in Cape Province. Lake Adelaide (altitude 1220 m) was the only water for which plantings were recorded.

In the early 1950's, Peak Timber Limited made several unsuccessful attempts to establish rainbow trout in the Popanyani River. However, beginning about 1954, the Komozane River (altitude 910 m) was stocked, and fish up to 1.4 kg were recovered until stocking ceased in the late 1960's.

Between 1954 and 1968 the Usutu Pulp Company planted rainbow trout reared in their own hatchery from ova obtained from Lydenburg Hatcheries in the Transvaal. At present 12 reservoirs are stocked with the species.

Trout farming is presently being initiated privately in the high veld (altitude 1500 m) in a hatchery with an anticipated animal capacity of 100,000 finished trout (Clay MS 1972).

ASIA

Afghanistan — Despite an earlier report of the probable presence of rainbow trout in Afghanistan waters, a recent investigation of the fish fauna has not found any rainbow trout (Naumann personal communication).

Indonesia — Rainbow trout were shipped from the Netherlands to Indonesia in 1929 and reared at Tjobanrondo near Malang. Survival in the hatchery was negligible. A second consignment of eggs, received from the Netherlands soon after, was hatched and the fry released into streams of the Kewi Mountain in East Java. However, there has been no survival (Schuster 1950).

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Iran — Rainbow trout were introduced into Iran about 1966 and are now cultured in two private hatcheries, one at Karadj and the other on the Jejerud River. Production is essentially for the commercial fish market in Tehran but a few fish are released in the Karadj reservoir (Kinumen personal communication).

Waters suitable for the species in Iran would seem to be restricted to the Elborz mountain range except for the Ligran-chay River in Azarbaijan Province. The present distribution of rainbow trout is restricted to the southerly flowing Karadj and Jejerud rivers and their respective reservoirs, and to the Namrud and Mader-su rivers flowing towards the Caspian Sea. Only a small population occurs in the Ligvan-chay River. While the trout do not reach a large size in the streams, fish up to about 5 kg are produced in the reservoirs (Kinumen personal communication).

Korea — The original paper documents the propagation of rainbow trout in Korea since 1965. As a matter of record, the species was first introduced to Korea in 1945 by the importation of 120,000 eggs. This stock was reared in provinces in northern and southern parts of the country. During the war, the rainbow trout in the south (Republic of Korea) died, but survived in the north (Korean People's Democratic Republic) (Peng 1957) and are considered to be still present.

Népal — More specific details on the recent propagation of rainbow trout in Népal have been provided by Woynarovich (personal communication). Two fish survived from the original shipment from Japan to the Godavark fish farm in 1969. As well, a few rainbow trout were included in a consignment of 300 brown trout obtained from Kashmir in the same year. By January 1971 only seven rainbow trout survived but 850 eggs were procured from a single female from which 400 yearlings are being held to provide brood stock for a newly-constructed trout farm at Trisuli, northwest of Katmandu. Plantings into natural waters are planned.

Pakistan and Kashmir — Rainbow trout do not exist within the present boundaries of West Pakistan (Husain, Sheri personal communications). Distributional data given in the original paper applies to the disputed province of Kashmir where the original plantings were made by the Pakistanis.

AUSTRALASIA

Tasmania — The statement in the original paper that "self-sustaining populations of rainbow trout occur in most streams of Tasmania" was meant to include only those waters named as being environmentally suited for survival of the species.

Papua and New Guinea — The initial attempt to introduce rainbow trout to the Territory was made in 1956 when 50,000 eggs were brought from Australia to Goroka but died during incubation. Attempts made in 1956 and 1959 were apparently unsuccessful. The 1964 planting noted in the original paper consisted of 2000 fry received from Jindabyne, New South Wales.

In 1970, 800 fry imported from New South Wales were planted in the Erave and Tari Kikori river systems. In 1971, 17,750 fingerlings reared at Mendi were released in the Mendi-Erave, Tua-Erave, and Waga-Kikori systems and in lakes Egari and Pipiak near Mendi (Conroy personal communication).

EUROPE

Albania — Although rainbow trout were reported to be present in Albania at an earlier date, the species was introduced officially to the country in 1971 (Pillay 1971). Stock was obtained from Vrutok in Macedonia, Yugoslavia, and reared in the Albanian fish culture station at Tushemishta near Lake Ohrid. Further details are unknown.

NORTH AMERICA

The United States — While the establishment of self-sustaining populations of rainbow trout in Alabama remains unlikely, recent attempts to culture the species in the brackish waters of Dauphin Island, 4 miles offshore, during the cooler winter months have been encouraging (Tatum 1972).

The annual stocking rate for rainbow trout in California was given in the original paper (Table 1) as 13 million fingerlings annually. The current annual stocking rate is about 21 million fingerlings and subcatchables (under 7.5 inches in length) and 9½ million catchable trout (Bruley 1971; Shapovalov personal communication).

Rainbow trout were first introduced to Florida in 1950 (Duncan and Meehean 1953). While brown trout and brook trout (*Salvelinus fontinalis*) were planted also for several years, plantings since the late 1950's have been exclusively rainbow trout released in spring-fed lakes and streams on the Elgin Air Force Base in Okaloosa and Santa Rosa counties of northern Florida. However, the populations are not self-sustaining (Swift, Bess personal communications).

With reference to Fig. 2 in the original paper, the naturalized population of rainbow trout in Texas should be located on the west side of the Pecos River (Hubbs personal communication).

Panamá — Rainbow trout were first transferred to the Río Chiriquí in western Panamá at an altitude of about 1500 m (Hildebrand 1935, 1938) in 1925 rather than 1932. This early planting and subsequent plantings in 1932, 1933, and 1950 with

fish provided by the United States Bureau of Fisheries resulted in the establishment of breeding populations in both the Chiriquí and Caldera Rivers of the El Volcan de Chiriquí. Releases were made in 1968 and 1969 in various lakes, rivers, and streams of the Volcan–Boquete area but the results have not yet been appraised (Howard personal communication).

West Indies — In addition to those plantings previously reported for Cuba, Puerto Rico, and the Dominican Republic, trout fingerlings presumed to have been rainbow trout were introduced to Haití sometime prior to 1953 (Bonnefil, Erdman personal communications). Releases were made in the mountain stream of Bassin Bleu and other streams in southern Haiti north of Les Cayas in the "pine country". Further information is not available.

Discussion

Subsequent correspondence and discussion since publication of the original paper (MacCrimmon 1971) confirm a general acceptance of the limits of the native and introduced range of the rainbow trout as described therein. Modifications in the known world distribution presented in this note (Fig. 1) are of modest significance beyond providing further documentation of failures and successes in extending the naturalized range of the species.

Because of the popularity of the rainbow trout as an experimental fish in biological laboratories, the species has been distributed almost universally for this purpose among universities and research agencies and, as a result, extensive literature has been published dealing especially with salmonid taxonomy and with the physiology and behaviour of experimental trout. As noted in the original paper, the application of laboratory findings to rainbow trout management have been hampered by only limited ecological studies in natural environments. However, the demand for hatchery-reared rainbow trout for live release and domestic sale has advanced greatly the artificial culture of the species through the application of scientific findings, especially in the areas of pathology and nutrition.

The extensive world distribution of the rainbow trout may be explained by a combination of favorable biological, social, and economic factors. Firstly, the species lends itself remarkably well to artificial culture, with an inherent ability to adapt itself to a variety of hatchery situations. Consequently, the only restrictions on the volume of hatchery production are water supply, water temperature, and holding facilities. Such environmental conditions are available over a surprisingly large part of the earth's surface ranging from the subartic through the temperate zones to the mountainous regions of the tropics. The reader is referred to the original paper (MacCrimmon 1971) for a synthesis of the environmental requirements of rainbow trout.

Secondly, there is almost universal acceptance of the rainbow trout as a sport fish. Whether the

FIG. 1. Known world distribution of rainbow trout (*Salmo gairdneri*). Native range indicated by shaded area; naturalized range, by solid areas.

populations are self-sustaining or sustained by repeated releases of hatchery-reared fish on a "put-take" basis, whether it be the large anadromous steelhead of large lakes and marine environments or the smaller specimens in mountain streams and fish ponds, the rainbow trout is a recreational product for which there is an ever-increasing angler demand.

Thirdly, the trout farming industry has come to rely on the rainbow trout to provide the bulk of the domestic production, at least for the time being. The need for stocks of the species to supply a growing world market has necessitated an almost continuous local and international exchange of eggs among trout farmers. The origins of most strains of trout have been lost in the continuing shuffle of fish among both government and private hatcheries and this account of the world distribution of the rainbow trout has made no attempt at identification below the specific level although it is recognized that genotypic and phenotypic differences no doubt occur (Bidgood and Berst 1967). While the trout farming industry has played a significant role in extending the world distribution of rainbow trout, it must also assume a responsibility along with government agencies for the spread of communicable fish diseases which threaten the welfare of both domestic and wild fish.

Because of the remarkable public acceptance of the rainbow trout as a sport and food fish, the species has become an economic asset in virtually all of these areas of the world offering it suitable environmental conditions whether in hatcheries, impoundments, or natural waters. While the economic benefits to tourism and the food industry may be expected to intensify the production and use of the rainbow trout on a local and world basis, a significant extension of the present world range is unlikely because of environmental limitations.

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Food of Pacific Hake (*Merluccius productus*) on an Offshore Bank Southwest of Vancouver Island, British Columbia

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OUTRAM, D. N., AND C. HAEGELE. 1972. Food of Pacific hake (*Merluccius productus*) on an offshore bank southwest of Vancouver Island, British Columbia. J. Fish. Res. Bd. Canada 29: 1792–1795.

In 1196 adult Pacific hake (*Merluccius productus*) stomachs from off the British Columbia coast euphausiids occurred in 94%; Pacific sandlance (*Ammodytes hexapterus*) in 26%; Pacific herring (*Clupea harengus pallasii*) and eulachon (*Thaleichthys pacificus*) each 5%; and lanternfish, young rockfish, northern anchovy (*Engraulis mordax*), and pandalid shrimp each in 3% or less. Fish, particularly herring, were of greater importance in the diet of larger hake. The extent of stomach fullness and the stage of digestion of stomach contents were similar for all sizes of hake taken in daylight tows. The presence of fresh to near-fresh organisms in only 9% of the stomachs, coupled with large numbers (52%) of empty to near-empty stomachs, indicated low feeding activity during daylight hours.

OUTRAM, D. N., AND C. HAEGELE. 1972. Food of Pacific hake (*Merluccius productus*) on an offshore bank southwest of Vancouver Island, British Columbia. J. Fish. Res. Bd. Canada 29: 1792–1795.

Parmi 1196 estomacs de merlus du Pacifique adultes (*Merluccius productus*) provenant du large de la Colombie-Britannique, les euphausides sont présents dans 94%, le lançon du Pacifique (*Ammodytes hexapterus*) dans 26%, le hareng du Pacifique (*Clupea pallasii*) et l'oulachon (*Thaleichthys pacificus*) chacun dans 5%, les lanternes, les jeunes perches de mer, l'anchois septentrional (*Engraulis mordax*) et les crevettes pandalides chacun dans 3% ou moins des estomacs. Les poissons, surtout le hareng, prennent plus d'importance dans le régime à mesure que le merlu grossit. Chez les merlus capturés de jour, le volume et le stade de digestion du contenu stomacal sont les mêmes, quelle que soit la taille. La présence d'organismes frais ou presque frais dans seulement 9% des estomacs, en plus d'un grand nombre (52%) d'estomacs vides ou presque vides, démontrent que le merlu se nourrit très peu de jour.

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LARGE concentrations of Pacific hake (*Merluccius productus*) occur over the continental shelf from southern Vancouver Island to northern Oregon. Little is known about the food habits of hake off the British Columbia coast. Stomach samples were acquired with daily to twice daily daylight hauls from a research trawler fishing 30 miles south of Barkley Sound (125°00′–125°30′W long., 40°15′–48°4′N. lat.), Vancouver Island, British Columbia. Fishing methods and other biological data obtained during this cruise are given in Fisheries Research Board of Canada Technical Report 210 (Westrheim et al. MS 1970).

Materials and methods — From 45 to 134 hake per tow were processed at sea and for each fish fork length to the nearest lower centimeter was recorded. The stomachs were examined for content, fullness, and state of digestion of the contents. Items of diet were classified by species whenever possible and their frequency of occurrence determined. Stomach fullness was rated as one of six categories from empty to full and the state of digestion of stomach content as one of five categories from fresh to fully digested. Hake sizes were divided into three 10-cm length-groups to determine if stomach content, fullness, or state of digestion of contents change with predator size.

During the cruise a total of 4288 hake were sampled for size composition of the catches with stomach analysis being undertaken on 1593 fish. The size range of the total sample was 42–72 cm and the mean length 56.1 cm (Westrheim et al. MS 1970, Table 2). The size range of the stomach analysis group was 42–71 cm and the mean length 56.2 cm. Thus, the hake sample processed for stomach analysis was representative with respect to size composition of the total catch.

Stomach contents — Of the 1196 stomachs with food 94% contained euphausiids; 26% Pacific sandlance (*Ammodytes hexapterus*); 5% eulachon (*Thaleichthys pacificus*); 5% Pacific herring (*Clupea*

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TABLE 1. Analyses of hake stomachs examined during GBR 70-2, August 1970.

Time of tow (PDT)							% frequency of 1196 stomachs with food containing							Degree of stomach fullness (% of total no. of fish, 1593)						Degree of digestion (% of total no. of stomachs with food, 1196)				
Start	End	Date (1970) Aug.	Tow no. and net used[a]	No. of stomachs sampled	No. of stomachs with food		Euphausiids	Pandalid shrimp	Sandlance	Eulachon	Herring	Northern anchovy	Mixed[b]	Empty	¼ full	⅜ full	½ full	¾ full	Full	Fresh	¼ digested	½ digested	¾ digested	Fully digested
							A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R
0825	0924	15	12(U)	45	35		94	11	14	6	3	–	–	22	30	22	13	13	–	–	11	66	23	–
0940	1025	12	7(U)	96	74		96	11	24	–	–	1	1	23	37	16	15	6	3	–	8	51	38	3
1040	1133	17	16(E)	100	73		99	1	21	3	1	–	1	27	45	17	6	4	1	–	7	36	49	8
1107	1141	14	10(U)	134	111		96	4	28	3	2	2	2	17	13	27	28	11	4	2	4	52	41	1
1110	1238	18	19(E)	99	77		93	3	16	8	19	–	3	22	25	18	13	12	10	–	6	36	51	7
1238	1325	12	8(U)	70	51		94	6	29	4	–	–	4	27	29	14	27	2	1	8	2	45	39	6
1259	1338	19	22(E)	92	66		92	2	11	–	15	–	–	28	28	20	15	6	3	3	14	21	61	1
1303	1342	11	5(U)	99	82		94	2	60	–	1	–	4	17	15	43	12	9	4	2	26	39	28	5
1312	1358	15	13(U)	114	85		99	–	9	4	–	–	4	25	18	26	19	8	4	–	2	56	40	2
1341	1402	17	17(E)	105	70		86	3	31	24	3	1	3	33	28	21	11	4	3	9	7	37	38	9
1416	1450	16	15(E)	108	76		87	–	30	26	1	–	3	30	21	24	16	6	3	3	6	49	37	5
1427	1504	18	20(E)	127	101		96	1	19	–	14	–	4	20	31	21	13	7	8	1	4	38	52	5
1437	1457	14	11(U)	114	89		97	1	21	–	2	–	3	22	23	31	18	2	4	1	3	58	36	2
1438	1541	12	9(U)	84	65		91	6	26	–	6	2	2	23	39	17	10	6	5	–	8	35	43	14
1554	1627	15	14(U)	103	70		99	–	3	1	1	–	3	32	30	21	13	2	2	–	3	43	47	7
1553	1703	11	6(U)	103	71		89	7	66	–	–	1	6	31	26	19	8	6	10	4	3	64	25	4
			Total	1593	1196	%	94	3	26	5	5	1	3	25	27	23	15	6	4	2	7	45	41	5
						No.	1124	38	309	56	54	6	32	397	424	362	240	102	68	23	83	540	493	57

[a]U = Universal Mark II; E = Engel trawl.
[b]Lanternfish, young rockfish, and remains.

harengus pallasii); 3% mixed lanternfish, young rockfish, and unidentifiable fish remains; 3% pandalid shrimps; and 1% northern anchovy (*Engraulis mordax*) (Table 1). Traces of squid and kelp were found in a few stomachs. Alton and Nelson (1970) indicated euphausiids and fish were the main items of diet of Pacific hake caught off the coast of Washington and Oregon while Gatshall (1969) found ocean shrimp and euphausiids to be the dominant food items of hake along the coast of northern California. Best (1963) described Pacific hake off the California coast as opportunistic feeders preying on whatever is available.

Feeding habits did not change appreciably with hake size. Euphausiids were the most numerous food item of both large and small adult hake, although the percentage frequency of occurrence declined with increasing size of hake from 75.5% of total stomachs in the smallest (42–51-cm) size-group to 68.9% in the middle (52–61-cm) size-group and to 61.3% in the largest (62–71-cm) size-group. Schooling fish (sandlance, herring, eulachon, and northern anchovy) increased in frequency of occurrence from 21.8% to 26.0% to 34.4% from the smallest to the largest size-group. In particular, the incidence of herring rose from 0.6% to 2.8% to 15.1%.

Stomach fullness — Of 1593 stomachs examined, 52% were empty to one-fifth full (Table 1, columns H and I) with only 10% full to four-fifths full (Table 1, columns L and M). The proportion of full to near-full remained low and of empty to near-empty stomachs high throughout the daylight hours (Fig. 1). For all three 10-cm length-groups of hake the percentages of empty to one-fifth full and of full to four-fifths full stomachs were similar and ranged from 50.0 to 54.9% and from 8.7 to 14.5%, respectively. The frequency of occurrence (percent of total stomachs) of stomach fullness by 10-cm length-groups was:

Length-group (*cm*)	No. of fish	Fullness					
		Empty	$\frac{1}{5}$	$\frac{2}{5}$	$\frac{3}{5}$	$\frac{4}{5}$	Full
42–51	173	28.9	26.0	24.8	11.6	6.4	2.3
52–61	1330	24.1	26.9	22.7	15.6	6.5	4.1
62–71	90	28.9	21.1	18.9	16.7	4.4	10.1

The relatively large percentages of empty to near-empty stomachs combined with the small numbers of full to near-full stomachs indicate a general low level of feeding activity during daylight hours. Alton and Nelson (1970) also found a high incidence (50–53%) of empty hake stomachs 8–13 hr after sunrise, suggesting that hake are primarily nocturnal feeders.

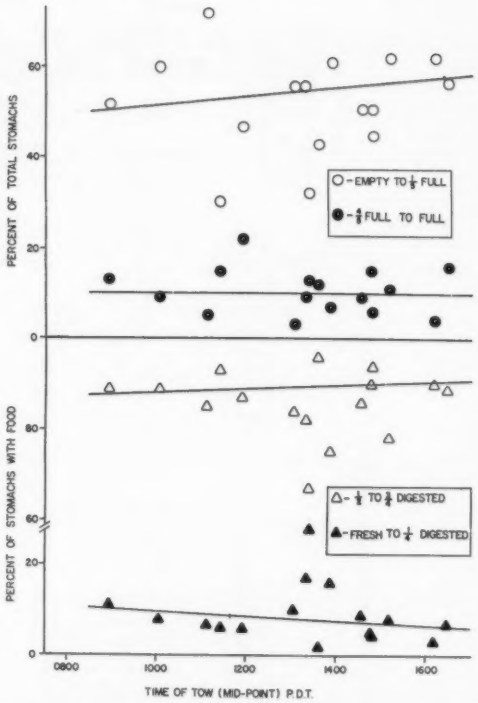

FIG. 1. Stomach fullness and state of digestion of stomach contents by time of day of trawl-caught hake, August 1970 (Regression lines fitted by eye).

State of digestion of contents — Of the stomachs with food, only 2% showed fresh contents (Table 1, column N) while 86% had contents one-half to three-quarters digested (Table 1, columns P and Q). Throughout daylight hours the number of stomachs with fresh to one-quarter digested food remained low (Fig. 1), indicating further that hake were not feeding to any great extent during the hours of daylight. The frequency of occurrence (percent of stomachs with food) of the states of digestion by 10-cm length-groups was:

Length-group (*cm*)	No. of fish	Fresh	Digested			
			$\frac{1}{4}$	$\frac{1}{2}$	$\frac{3}{4}$	Fully
42–51	123	0.8	12.3	45.9	34.4	6.6
52–61	1008	2.0	6.4	45.8	41.3	4.5
62–71	64	1.6	1.6	34.4	56.2	6.2

For all three 10-cm length-groups, 80.3 to 90.6% of the stomachs showed contents in a similar digestive condition, one-half to three-quarters digested.

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Recent Articles on FRB Investigations Published in Other Periodicals

Until 1970, reprints of these articles had been included in an annual volume of "Studies," composed of two parts. The final binding was the 1969 Studies, Part 2, which included No. 1355. These are no longer bound and distributed. We continue, however, to number and list all articles, which henceforth may be obtained in reprint form only from the author or originating FRB establishment. The number following each title refers to the FRB establishment listed below.

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Halifax Laboratory
P.O. Box 429
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Editorial Practices

Abstracts should be provided in both English and French.

The *Style Manual for Biological Journals* (2nd ed. American Institute of Biological Sciences, 2000 P St. NW., Washington, D.C.) is, with few exceptions, used as the authority in matters of form. *Webster's Third New International Dictionary* is the standard for spelling and division of words in English; *le Grand Larousse Encyclopédique*, for those in French. Exceptions are made for manuscripts that follow the *Oxford English Dictionary* entirely. Titles of periodicals are abbreviated as in the *Biological Abstracts* list. References to literature are made by the name-and-year system. Manuscript reports are included in the list of references, but are identified both there and in the text by the letters "MS" before the year. The *Journal* follows the spelling recommended in *A List of Common and Scientific Names of Fishes from the United States and Canada* (Third Edition, 1970), Special Publication No. 6 of the American Fisheries Society.

Notes are distinguished from *papers* on the basis of scope or completeness, rather than quality, of the research. They may be on problems with narrow, readily defined limits; on fishing gear or methods, or research techniques; on advances in knowledge arising as by-products of broader studies; on progress in projects that were discontinued before completion; or on preliminary findings that warrant publication before problems are resolved satisfactorily. Or they may be used to establish priority in publication. They may be organized with as much flexibility as papers except that they may have no centered headings. They should take no more than four pages in the *Journal*.

In general, *series titles* should be avoided.

Illustrations

Line drawings are preferably made with black india ink on white drawing or tracing paper or on coordinate paper with blue grids. All lines, symbols, letters, and numerals must be neat, and legible when the illustration is reduced to the appropriate size. Drawings should be grouped, when feasible, for economy of space. Originals must be submitted and should be less than 20 inches in the greater dimension for full-page illustrations, and proportionately smaller for those taking less than a page. Drawings must not be rolled for mailing.

Prints of photographs should be made on glossy paper with a wide range in tone. They should be cropped, squared, and mounted with rubber cement on white cardboard, with no space between those arranged in groups.

Proofs and Reprints

Galley proof is sent to the author, and he is responsible for detecting errors in printing as well as in content.

Fifty reprints, without covers, are supplied free. Additional copies needed must be ordered, on the form provided, when the galley proof is returned.

Checklist on Manuscripts

Attention to the following questions will expedite appraisal of manuscripts by referees and editors. The same questions are recommended to referees who review manuscripts for the *Journal*.

General

Is there new knowledge in the report worth publishing?
Are the findings, interpretations, and conclusions sound, and relevant to the purpose of the study?
If the manuscript is merely confirmatory, is it worth publishing?

Does the manuscript need to be rewritten before the work can be assessed?

Is the contribution placed in the proper perspective concerning the state of knowledge of the subject?

Is the manuscript too long?
Are all the tables and figures needed, and organized for economy of space?
Would any of the text be clearer if condensed?
Should some of the data be made available separately, in a manuscript report or at a data repository?
Should the manuscript be condensed as a Note?

Does the organization of the manuscript follow logically from the statement of purpose in the introduction?

Are summary statements given at the beginnings of sections and paragraphs, and are details in sections and paragraphs relevant to their topics?

Are there inconsistencies between tables or figures and the text, or within the text?

If the manuscript is from a thesis, does it retain characteristics common in these but not desirable in journals?

PARTS OF THE MANUSCRIPT

Does the *title* encompass the content of the report?

Does the *abstract* give the essentials of the new knowledge?

Has the *introduction* all the important guideposts for orienting the reader?

Is review of the literature limited to defining the problem?

Are details of *materials and methods* limited to what scientists need in understanding the design of the study and in judging adequacy of the data obtained?

Are generalizations on the *results* adequate?

Are findings distinguished from inferences from them?

Is *discussion* limited to interpretation and significance of the findings?

If there are loopholes in interpretation, are they acknowledged? Should they be overcome?

Should other interpretations be recognized?

Journal Fisheries Research Board Canada

Guide des auteurs

Des détails sur le tapage et certains autres item sont donnés dans le "Guide pour les secrétaires d'auteurs." Aussi, une liste d'épellations recommandées d'environ 100 mots relatifs aux articles sur les pêcheries est disponible au bureau du Directeur de la publication.

Disposition générale

Les résumés doivent être fournis en anglais et en français.

Le *Style Manual for Biological Journals* (deuxième édition, publié par l'American Institute of Biological Sciences, 2000, rue *P* N.-O., Washington, D.C.), a été adopté comme guide des auteurs. Le *Third New International Dictionary* de Webster, dans le cas de l'anglais, et le *Grand Larousse Encyclopédique*, dans le cas du français, font respectivement autorité pour l'orthographe et la séparation des mots. Une exception est faite à l'égard des travaux en anglais qui se conforment entièrement à l'*Oxford English Dictionary*. Les titres de périodiques sont abrégés selon la *Biological Abstracts*. Toute référence à la littérature doit suivre le système nom-année. Les rapports manuscrits sont inclus dans la liste des références, les lettres "MS" avant l'année les identifient dans les références et dans le texte. Le *Journal* se sert des épellations recommandées dans *A List of Common and Scientific Names of Fishes from the United States and Canada* (Troisième édition, 1970), Publication spéciale No 6 de l'American Fisheries Society.

Les *notes* se distinguent des écrits d'après l'étendue de la recherche plutôt que par la qualité de la recherche. Les notes peuvent être sur des travaux de recherche de portée restreinte, susceptibles de découler d'investigations plus considérables, pour la description de techniques de recherche et de méthodes de pêche, pour l'établissement de priorités de publication, et pour faire connaître les renseignements utiles tirés d'entreprises qui ont été interrompues avant d'avoir été achevées. Si la portée de la Note le permet, elle peut être disposée comme un mémoire. D'autre part, la disposition est flexible. La longueur ne doit pas dépasser quatre pages imprimées.

En général, les mémoires en série doivent être évités.

Les illustrations

Les dessins au trait doivent être exécutés à l'encre de chine sur papier à dessin blanc ou sur papier à calquer, ou sur papier à coordonnées avec quadrillage bleu. Les lignes, les symboles, les lettres et les chiffres doivent tous être propres. Ils doivent être lisibles quand ils sont réduits à la grandeur voulue pour la reproduction désirée. Les dessins doivent être groupés, si la chose est possible, de façon à utiliser tout l'espace disponible. Les originaux doivent être soumis et devraient mesurer moins de 20 pouces dans le sens le plus long pour les illustrations de pages entières, et proportionnellement plus petit pour les illustrations de moins d'une page. Les dessins doivent être postés à plat.

Les épreuves des photographies doivent être tirées sur papier glacé et accuser une gamme étendue de teintes. Elles doivent être coupées, dressées et montées, au moyen de dissolution, sur carton blanc, sans laisser d'espace entre celles qui sont disposées par groupes.

Epreuves et tires a part

Les épreuves en placards sont adressées à l'auteur et la responsabilité de toute erreur qui peut y rester lui incombe.

Cinquante tirés à part, sans couverture, sont fournis gratuitement. L'auteur peut profiter du renvoi des épreuves en placards pour commander d'autres tirés à part.

Liste de contrôles pour manuscrits

Une attention particulière portée sur les questions suivantes facilitera l'évaluation des manuscrits par les arbitres et les rédacteurs. Les mêmes questions sont recommandées aux arbitres qui font la critique des livres pour le *Journal*.

Generalites

Est-ce que les connaissances nouvelles du rapport méritent d'être publiées?

Les découvertes, les interprétations et les conclusions sont-elles solides et pertinentes au but de l'étude?

Si le manuscrit est tout simplement corroboratif, mérite-t-il d'être publié?

Le manuscrit doit-il être récrit avant d'évaluer le travail?

La contribution est-elle placée dans une perspective appropriée relative à l'état des connaissances du sujet?

Le manuscrit est-il trop long?

Les tables et figures sont-elles toutes nécessaires et arrangées pour économiser le plus d'espace?

Le texte serait-il plus clair s'il était condensé?

Est-ce qu'une partie des données devrait être disponible séparément, soit dans un rapport ou dans un dépôt des données?

Le manuscrit devrait-il être condensé en une note?

Est-ce que la préparation du manuscrit suit la logique mentionnée dans l'introduction?

Y a-t-il des exposés sommaires au début de chaque section et paragraphe, et les détails de ces sections et paragraphes sont-ils pertinents aux sujets?

Y a-t-il des contradictions entre les tableaux et les figures du texte, ou dans le texte même?

Si le manuscrit est tiré d'une thèse, contient-il des caractéristiques communes à cette dernière, mais indésirables dans un journal?

PARTIES DU MANUSCRIT

Le titre renferme-t-il le contenu du rapport?

Le résumé donne-t-il l'essentiel des connaissances nouvelles?

L'introduction a-t-elle tous les points importants afin d'orienter le lecteur?

Le renvoi bibliographique se limite-t-il à la définition du problème?

Les détails du matériel et des méthodes employées sont-ils limités à un minimum pour que les scientifiques comprennent le but de l'étude et puissent porter un jugement adéquat sur les données obtenues.

Les généralisations sur les résultats sont-elles adéquates?

Les conclusions sont-elles déduites des résultats?

La discussion est-elle limitée à l'interprétation et la signification de ces découvertes?

S'il y a des échappatoires dans l'interprétation, sont-elles reconnues? Devraient-elles être maîtrisées?

Devrait-on accepter d'autres interprétations?

Journal Fisheries Research Board Canada

Guide for Typists Preparing Copy

Read the "Guide to Authors" in the current volume of the *Journal*. When in doubt about how to type or arrange details, follow *Journal* practice.

Type the manuscript on white bond paper, not flimsy, preferably size 8.5 × 11 inches (21.5 × 28 cm). If possible, use paper with the lines numbered in the margin. Leave all margins at least 1 inch (2.5 cm) wide. Use a nylon or carbon ribbon and keep the typewriter keys clean.

Double-space all parts of the manuscript, including tables, captions for illustrations, footnotes, and the reference list. Underline only material that is to be printed in italics. Indent the first line of each paragraph in the text and of each footnote.

In titles and headings, capitalize only the first word and proper names and adjectives. For small capitals, use small letters.

Indicate all text footnotes by superscript arabic numbers. Number them consecutively throughout the manuscript, starting with those on the title page. Place each footnote immediately below the reference to it, separating it from the text by horizontal lines.

On the first page type only the title, the authors' names and affiliations, related footnotes, and the running head (Appendix A). Type the abstract on a separate page (Appendix B). Number all pages, beginning with the title page and including those for tables and captions for illustrations.

Have the author check the finished manuscript, and send two copies (the ribbon copy and a carbon copy or a photocopy) to the Office of the Editor.

Tables

Examine the current volume of the *Journal* to see how tables are set up (Appendix C).

Note especially the following concerning *numbered tables*:

Type each table on a separate page, using paper without the lines numbered.

Number the tables with arabic numerals.

Use horizontal lines above and below the headings and below the columns, and seldom elsewhere. Never use vertical lines; leave extra spaces instead.

Indicate table footnotes by superscript small letters and type them below the table.

Place the tables after the list of references.

Where each table is first referred to, type in the margin "Table — near here."

Note that *text tables* are not numbered, they are typed with the text, they seldom need horizontal lines, and the data are arranged in as few rows as possible (Appendix C).

Illustrations

Send the original and two clear copies of each illustration with the manuscript. At the lower left of each figure and copy, give the author's name and the figure number. Also type each caption with its figure for identification. For photographs, type this information on a strip of paper and fasten it to the back of the print. Do not write or type on the print itself. Also, type the captions in succession on a separate page, headed "Captions for illustrations." Put this page at the end of the manuscript.

Where each figure is first referred to, type in the margin "Fig. — near here."

Mathematical Expressions, Equations, and Formulas

Leave three spaces above and below lines that have much material in superscripts or subscripts, and above and below equations and formulas. In the various expressions, place each component in its correct position (Appendix D).

Show all symbols clearly. In the margin, spell out Greek letters the first time they occur, and distinguish between the small letter l and the numeral one, and between the capital letter O and the numeral zero. Make other explanatory notes similarly.

References

Check the text to see that all references in the list are referred to. Type the reference list, double-spaced, in the style that is used in the *Journal* (Appendix E). Names of journals are abbreviated as in the *Biological Abstracts* list, but if an abbreviation is in doubt, type the name in full.

Spellings

A list of about 100 words common in fisheries journals is given in Appendix F.

Appendices

Appendices A to F are available on request from the Office of the Editor.

Journal Fisheries Research Board Canada

Guide pour les secrétaires d'auteurs

Lisez le "Guide des auteurs" dans l'édition courante du *Journal*. Si vous avez des doutes sur la façon de taper ou d'arranger les détails, suivez la pratique du *Journal*.

Tapez le manuscrit sur un papier blanc et non un papier pelure, mesurant de préférence 8½ × 11 po. (21.5 × 28 cm) et laissant une marge d'au moins 1 po. (2.5 cm). Si possible, employez un papier avec des lignes numérotées dans la marge. Employez un ruban nylon ou carbone et gardez les clés du dactylo nettes.

Chaque partie du manuscrit doit être tapée à double-interligne au moins. La chose est particulièrement importante dans le cas des tableaux, légendes d'illustrations, renvois au bas de la page et listes de références bibliographiques. Evitez de souligner à moins que la matière ne soit en italique. Mettez en retrait la première ligne de chaque paragraphe du texte, ainsi que de chaque légende et renvoi.

Dans les titres et en-têtes, n'employez la majuscule que pour le premier mot, les noms propres et les adjectifs. Pour les petites majuscules, utilisez les petites lettres.

Indiquez tous les renvois au texte par des chiffres arabes en-tête. Numérotez-les consécutivement à travers le texte en commençant par ceux de la page-titre. Placez chaque renvoi immédiatement sous sa référence, le séparant du texte par des lignes horizontales.

La première page ne doit donner que le titre du sujet, le nom et l'affiliation de l'auteur ou des auteurs, et tout autre renvoi utile (Appendice A). Tapez le résumé sur une page séparée (Appendice B). Numérotez chaque page, débutant avec la page-titre.

Voyez à ce que l'auteur vérifie le manuscrit final, et soumettez la première copie et un double du travail au Directeur de la publication.

Tableaux

Consultez une copie du *Journal* pour savoir composer les tableaux et placer les lignes qui y entrent (Appendice C).

Portez une attention particulière à ce qui suit concernant les *tableaux numérotés*.

Tapez les tableaux sur des pages séparées, en utilisant du papier sans lignes numérotées.

Numérotez les tableaux avec des chiffres arabes.

Employez des lignes horizontales au-dessus et au-dessous des en-têtes et au-dessous des colonnes, et très rarement ailleurs. N'employez jamais de lignes verticales; de préférence, laissez de l'espace supplémentaire.

Indiquez les renvois dans les tableaux au moyen de petites lettres italiques en position supérieure et tapez-les au bas de la page.

Placez les tableaux après la liste de références.

A l'endroit où un tableau est mentionné pour la première fois, tapez dans la marge "Tableau (- - -) près d'ici."

Remarquez que les *tableaux dans le texte* ne sont pas numérotés, ils sont tapés avec le texte. Ils ont rarement besoin de lignes horizontales, et l'information est préparée de façons à prendre le moins de rangées possibles.

Illustrations

Joignez au manuscrit expédié le dessin original des illustrations et des photocopies en deux exemplaires.

Au bas et à gauche de chaque figure et photocopie, inscrivez le nom de l'auteur et le numéro de la figure. Aussi, tapez chaque légende avec sa figure pour fin d'identification. Pour les photographies, tapez l'information sur une lisière de papier et collez-la au dos de la photographie. N'écrivez pas et ne tapez pas sur la photographie même. Tapez ensemble sur une feuille séparée et par ordre consécutif les légendes des illustrations, et intercalez cette feuille à la suite du texte.

A l'endroit où chaque figure est mentionnée pour la première fois, tapez dans la marge "Fig. (- - -) près d'ici."

Equations, formules et expressions mathematiques

Laissez trois espaces au-dessus et au-dessous des lignes qui contiennent du matériel en positions supérieures ou en positions inférieures, et au-dessus et au-dessous d'équations et de formules. Dans les différentes expressions, placez chaque composante dans sa position appropriée (Appendice D).

Indiquez les symboles clairement. Dans la marge, épelez les lettres grecques la première fois qu'elles apparaissent et faites une distinction entre la lettre "l" et le chiffre "un" et entre la majuscule "O" et le

chiffre "zéro." Procédez de la même façon pour d'autres notes explicatives.

References

Vérifiez le texte afin d'assurer que sont mentionnées toutes les références ou renvois de la liste. Tapez, à doubles interlignes et de la façon prévue (Appendice E) pour le *Journal*, la liste de références. Les noms de journaux sont abrégés suivant la *Biological Abstracts*, mais s'il y a doute, écrivez le nom au long.

Vocabulaire

Une liste d'environ cent mots relatifs aux articles sur les pêcheries est disponible au bureau du Directeur de la publication (Appendice F).

Appendices

Les appendices de A à F sont disponibles sur demande au bureau du Directeur de la publication.

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Journal of the Fisheries Research Board of Canada

Volume 29, No. 12, December 1972 JFRBAK29(12)1665–1799(1972)

Announcement J. C. Stevenson 1665

Eggs and larvae of northern sand lance (*Ammodytes dubius*) from the Scotian Shelf J. S. Scott 1667–1671

Morphological and meristic variation in northwest Atlantic sand lances (*Ammodytes*) J. S. Scott 1673–1678

Evidence for expatriate populations of the lanternfish *Myctophum punctatum* in the northwest Atlantic R. E. Zurbrigg and W. B. Scott 1679–1683

Mercury concentration in relation to size in several species of freshwater fishes from Manitoba and northwestern Ontario D. P. Scott and F. A. J. Armstrong 1685–1690

Effects of various metals on survival, growth, reproduction, and metabolism of *Daphnia magna* K. E. Biesinger and G. M. Christensen 1691–1700

Growth, life history, and respiration of *Mysis relicta* in an arctic and temperate lake D. C. Lasenby and R. R. Langford 1701–1708

Morphological differences in male gonads among nine genera of Gadidae (Pisces) V. D. Vladykov 1709–1716

Size at maturity, fecundity, and embryonic growth of the spiny dogfish (*Squalus acanthias*) in British Columbia waters K. S. Ketchen 1717–1723

Effects of several factors on the growth of the American lobster (*Homarus americanus*) in captivity D. W. McLeese 1725–1730

Use of a commercial dredge to estimate a hardshell clam population by stratified random sampling H. J. Russell Jr. 1731–1735

Social interaction between juvenile coho (*Oncorhynchus kisutch*) and fall chinook salmon (*O. tshawytscha*) in Sixes River, Oregon R. A. Stein, J. D. Hall, and P. E. Reimers 1737–1748

Summer storage of energy and its use for winter metabolism and gonad maturation in American plaice (*Hippoglossoides platessoides*) J. C. MacKinnon 1749–1759

Notes

Size selection of *Daphnia pulicaria* by yellow perch (*Perca flavescens*) fry in West Blue Lake, Manitoba B. Wong and F. J. Ward 1761–1764

Sea lions wintering along the outer coast of Vancouver Island I. D. Smith 1764–1766

An instrument for measuring conductivity profiles in inlets D. M. Farmer and T. R. Osborn 1767–1769

Salmon-canning waste water as a microbial growth medium G. A. Strasdine and J. M. Melville 1769–1771

New complexities in zoogeography and taxonomy of the pygmy whitefish (*Prosopium coulteri*) C. C. Lindsey and W. G. Franzin 1772–1775

Two new host species for the parasitic fungus *Ichthyophonus hoferi* in the northwest Atlantic J. D. Hendricks 1776–1777

Mercury removal from fish protein concentrate L. W. Regier 1777–1779

Some physiological consequences of handling stress in the juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*) G. Wedemeyer 1780–1783

Device for measuring length and girth of fish C. J. Hunter and C. O. Wheeler 1784–1785

The representation of lower molecular weight fatty acids by the Bligh and Dyer extraction method R. E. Hurst 1786–1787

World distribution of rainbow trout (*Salmo gairdneri*): further observations H. R. MacCrimmon 1788–1791

Food of Pacific hake (*Merluccius productus*) on an offshore bank southwest of Vancouver Island, British Columbia D. N. Outram and C. Haegele 1792–1795

Recent articles on FRB investigations published in other periodicals 1797–1798

Additional FRB publications 1799

Guides to Authors and Typists *i–vii*

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